TIMING AND JUDGMENT IN THE DURATION BISECTION TASK: ELECTROPHYSIOLOGICAL ANALYSES

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DECLARATION

I hereby declare that this thesis is my original work and it has been written by me in its entirety. I have duly acknowledged all the sources of information which have been used in the thesis.

This thesis has also not been submitted for any degree in any university previously.

NG Kwun Kei

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TABLE OF CONTENTS

SUMMARY

The hypothesis that the Contingent Negative Variation (CNV), an event-related potential (ERP) component, is an electrophysiological correlate of the temporal accumulation process in the pacemaker-accumulator model of interval timing was examined in three experiments using the duration bisection task. In Experiment 1, the slope of the CNV amplitude change was statistically different from zero at time periods equal to the short anchor and the bisection criterion, durations that are critical for making a bisection judgment. However, the CNV amplitude did not differ between trials classified as more similar to the Short anchor and those classified as more similar to the Long anchor. These results are not fully consistent with the temporal accumulation account, since the CNV did not reflect temporal memory, nor is the account the only plausible explanation for the temporal decision making aspect of the CNV slope. In Experiment 2, the CNV showed different time courses depending on absolute duration length. Shorter durations resulted in a more negative CNV and better defined CNV ramp and peak than longer durations. These differences are not consistent with the proposal of a temporal accumulator with a fixed threshold that is manifest as the maximal CNV amplitude. Principal component analysis (PCA) on current source density (CSD) transformed data suggests that the CNV may reflect sustained temporal attention, which was stronger when the anticipated ending of the durations was earlier (i.e., shorter absolute durations). In Experiment 3, the same principal component could be extracted for both visual and auditory durations. This amodal component had a bilateral temporal/prefrontal topographical distribution rather than a fronto-central distribution. Although a motor preparation explanation cannot be excluded, its stronger projection on the right hemisphere is consistent with a previous fMRI study showing the association between temporal attention and the right prefrontal cortices. Overall, these results suggest that the CNV should not be interpreted as a physiological manifestation of temporal

accumulation, but rather processes that are contingent on or mediating timing mechanisms.

LIST OF FIGURES

LIST OF TABLES

Chapter 1 Introduction

The sense of time plays an indispensable role in life. Important cognitive abilities such as speech (Kotz & Schwartze, 2010; Schirmer, 2004) could not exist if humans were not sensitive to the temporal structure. At a wider time scale, the perceived magnitude of rewards and punishments are often modulated by time (Balci, Freestone, & Gallistel, 2009; Klapproth, 2008; Lawrence & Klein, 2013). The same amount of reward may be valued differently at different intervals due to temporal discounting (Balci et al., 2011). Decision making of this sort, known as temporal decision making or temporal risk management (Balci et al., 2011; Klapproth, 2008), guarantees maximal reward and minimal punishment only if behavior is elicited at the optimal duration (e.g., Hudson, Maloney, & Landy, 2008). For instance, prediction of outcomes based on time allows humans to allocate mental resources in advance to achieve faster reaction and better perception of the outcomes (Correa, Lupiáñez, Madrid, & Tudela, 2006; Coull & Nobre, 2008; Jones & Boltz, 1989). Conversely, misjudgment of time can hamper the quality of decisions (Kim & Zauberman, 2013); uncertainty in time induces stress (Monat, 1976); and poorer timing ability has been associated with less desirable personality traits (e.g., impulsivity; Wittmann et al., 2011) and pathologies (e.g., Parkinson's Disease; Allman & Meck, 2012; Kotz & Schwartze, 2011). Therefore, being able to perceive, encode, retrieve, and act upon a temporal duration is critical for normal functioning and survival in humans and non-human animals (Gallistel & Gibbon, 2000, 2002; Zarco, Merchant, Prado, & Mendez, 2009). Thus, better understanding of the timing mechanisms is of both theoretical and practical interest (e.g., Block & Gellersen, 2010; Buhusi & Meck, 2005; Johnston et al., 2008; Lustig & Meck, 2011).

Different time ranges encompass different cognitive processes and behaviors and may rely on different mechanisms (Lewis & Miall, 2006; Mauk & Buonomano, 2004). Specifically, many types of temporal decision-making are made within

hundreds of milliseconds and tens of minutes, termed interval timing. These durations can be cognitively mediated (e.g., under the influence of attention; Lewis & Miall, 2003a) and involve an extensive sensorimotor network in the brain (Penney & Vaitilingam, 2008). Numerous cognitive models have been constructed to explain how humans estimate durations. All successful timing models can account for the scalar property of time, i.e. the variability in estimated time being proportional to the mean estimation. They differ on how information is gathered to form a duration estimate, such as whether timing is clock-like (Gibbon, 1977; Treisman, 1963) or the result of the learning of behavioral states (Jozefowiez, Polack, Machado, & Miller, 2014). In particular, the pacemaker-accumulator model of Scalar Timing Theory (STT; Gibbon, Church, & Meck, 1984), the most widely cited information processing model of interval timing, comprises clock, memory, and decision stages. At the clock stage, a pacemaker emits pulses as time elapses, which are integrated in an accumulator when an attention-modulated switch (Penney, Allan, Meck, & Gibbon, 1998; Zakay, 2000) is closed. The number of pulses in the accumulator thus represents the subjective duration perceived by the subject. This representation is stored in working memory and long-term memory if needed. At the decision stage, the record in the accumulator is compared with relevant representations stored in reference memory. When the difference between the two is smaller than some threshold, they are treated as equivalent and a response is emitted.

Many cognitive models are built to describe how a cognitive function is executed in the human brain. Studying human cognition with neuroimaging techniques allows the examination of the plausibility and validity of such models *in vivo* (Davies, 2010; Mather, Cacioppo, & Kanwisher, 2013). These results in turn provide new evidence for refining existing cognitive theories (Eimer, 1998). In the domain of interval timing research, behavioral (Burle & Casini, 2001; Fortin & Massé, 2000; Ruthruff & Pashler, 2010) and neuroimaging evidence (Harrington et al., 2004;

Rao, Mayer, & Harrington, 2001; Rubia & Smith, 2004) favors the multistage view of time perception, with each stage implemented by different neural networks (e.g., Gooch, Wiener, Hamilton, & Coslett, 2011; Morillon, Kell, & Giraud, 2009). Neurons are also able to fire in patterns proposed in some of the interval timing models, making these models more favorable candidates for explaining actual timing mechanisms than their competitors (Janssen & Shadlen, 2005; Simen, 2012).

The pacemaker-accumulator model is attractive not only because it explains many behavioral patterns successfully, but also because a number of neuroimaging studies have reported supportive evidence of its physiological plausibility (Akkal, Escola, Bioulac, & Burbaud, 2004; Casini & Vidal, 2011; Kotz & Schwartze, 2011; Macar, Vidal, & Casini, 1999), although others have reported equivocal findings (Kononowicz & van Rijn, 2011). Recent years have seen reformulations of this powerful model (Simen, Rivest, Ludvig, Balci, & Killeen, 2013) and proposals for alternatives (e.g., Meck, Penney, & Pouthas, 2008). The present work contributes to this debate via use of electrophysiological measures of the brain while participants engaged in interval timing. The electroencephalogram (EEG) and its derivative the event-related potential (ERP) allow non-invasive recording of brain electrical potentials in humans with electrodes placed on the scalp (Luck, 2005) and have been used extensively to infer the mechanisms subserving interval timing (Brannon, Libertus, Meck, & Woldorff, 2008; Macar & Vidal, 2004). Among these EEG signals, the slow cortical potentials (SCP) span several hundreds of milliseconds to several seconds, and thus may underlie the establishment of inter-stimulus temporal relations in the hundreds of milliseconds to seconds range (e.g., see Birbaumer, Elbert, Canavan, & Rockstroh, 1990 and Macar & Vidal, 2004 for a review). As discussed in subsequent chapters, the Contingent Negative Variation (CNV) is argued to be a SCP that shows systematic changes in its features with manipulations of the temporal

relationships between stimuli. We examined to whether manifestations of the CNV are consistent with the hypotheses generated from the pacemaker-accumulator model.

We studied the EEG/ERPs when participants performed a duration bisection task in three experiments. Briefly, the task required participants to make a categorical judgment about the presented durations. An EEG study using this task should provide an opportunity for cross-validation of the evidence for the pacemaker-accumulator model (Merchant, Zarco, & Prado, 2008). Since the pacemaker-accumulator model makes specific hypotheses about the CNV profile, we examined whether the CNV changes are in line with these hypotheses in the bisection task.

The content is organized as follows.

Chapter 2 starts with a review of EEG/ERP and the relationship between timing and the contingent negative variation (CNV) proposed by various researchers. The bisection task and its similarity to other classical timing tasks is discussed next. The chapter concludes by summarizing the expected CNV changes in the subsequent bisection experiments. Chapters 3 to 5 discuss the methods and results of three experiments. Chapter 3 presents a revised analysis of Ng, Tobin, and Penney (2011), which attempted to generalize the CNV-timing association reported in S1-S2 paradigms to the duration bisection paradigm. Chapter 4 presents Experiment 2, which extended the results of Ng et al. (2011) by examining the time course of the CNV using two sets of durations with different ranges; if the CNV reflects an accumulator, both time courses should conform to the pacemaker-accumulator hypothesis. Chapter 5 reports Experiment 3, which was based on the 'sound is longer than light' effect (Wearden, Edwards, Fakhri, & Percival, 1998), the phenomenon that auditory duration is judged longer than its visual counterpart (Penney, Gibbon, & Meck, 2000). Chapter 6 comprises the General Discussion.

Chapter 2 EEG, the Contingent Negative Variation, and the Bisection Task

Brief Introduction of EEG and ERP

To search for the neural substrates of time perception, researchers have turned to various neuroimaging techniques. On one hand, many cognitive operations are unconscious and may not exert a direct effect on overt behavior. On the other hand, many competing cognitive models give radically different explanations for a phenomenon, yet both may fit the observed data equally well (Roberts & Pashler, 2000). For example, Parkinson's disease patients can perform an implicit motor timing task at comparable response times, although some of them are known to have timing deficits (Allman & Meck, 2012). Using electrophysiological recording, it is found that their neural systems can encode time normally, but cannot exploit this timing information for anticipation (Praamstra & Pope, 2007). Neuroimaging techniques thus allow more direct monitoring of mental chronometry (Posner, 2005) to complement its behavioral counterpart (Sternberg, 1969). Electroencephalography (EEG) tracks summated cortical activities in the milliseconds range, a temporal resolution desirable for understanding what happens when the brain gathers temporal evidence and issues a decision about brief time intervals.

The electroencephalogram (EEG) reflects the summation of excitatory and inhibitory post-synaptic potentials (EPSP and IPSPs) of multiple groups of neurons. Non-invasive scalp EEG records synchronized post-synaptic electrical signals from thousands of cortical pyramidal neurons oriented in an open-field configuration (Nunez & Srinivasan, 2006; Picton, 2006). Scalp-recorded EEG has excellent temporal resolution because it tracks instantaneous PSP summation, but has relatively poor spatial resolution because the signals are obtained from a limited subset of the active neurons (Srinivasan, Winter, & Nunez, 2006) and are subject to volume conduction of electrical signals (Luck, 2005). As a result, each recording site captures

a summation of activations from numerous local and distant neuron groups. This summation is not easily decomposed unless additional assumptions are made and advanced techniques are used (e.g., Handy, 2009; Michel, Koenig, Brandeis, Gianotti, & Wackermann, 2009).

The classical view of EEG, the evoked model (e.g., Hanslmayr et al., 2007; Yeung, Bogacz, Holroyd, & Cohen, 2004), states that recorded EEG potential contains both signal (due to experimental manipulations) and noise (due to task-irrelevant cognitive processes, as well as physiological and environmental artifacts). To enhance the signal and reduce noise, participants typically complete many trials for each experimental condition during the recording session. The averaging of the EEG across trials amplifies EEG features that are time-locked and phase-locked to the events of interest while suppressing the relatively random noise, at the expense of losing information regarding inter-trial variability (Dawson, 1951, 1954). The resultant average signal is termed an event-related potential (ERP). If certain features of the ERP (i.e., the peaks and troughs in the electrical signals) can be consistently identified by polarity, latency, scalp topography, and the eliciting conditions, such features are called components. ERP components are either transient (i.e., spanning a narrow time window and evoked by rapid changes such as a stimulus onset), or sustained (i.e., spanning several hundreds of milliseconds or more and are evoked by both rapid and gradual changes, Picton, 2006). Though termed as a component, an ERP component does not necessarily reflect a single perceptual or cognitive process. Overall, EEG/ERP gives a partial view of the electrophysiological signals generated from the brain; when supplemented with new analytic techniques and other neuroimaging methods, some of the limitations can be overcome, giving a more complete picture of the cognitive processes (e.g., Ahmadi & Quian Quiroga, 2013; McIntosh & Mišić, 2013; Pfurtscheller & Lopes da Silva, 1999; Ullsperger & Debener, 2010).

The CNV and Duration Estimation

In daily life, a lot of temporal information is present at the same time. How an individual extracts useful temporal information for adaptive behaviors is studied in the laboratory using tasks with more structured temporal information (see Grondin, 2001, 2010 for review). In prospective timing, participants are asked explicitly to estimate the magnitude of a duration or durations. Durations are primarily presented in the S1-S2 format, such that each trial comprises a standard – test duration pair. Participants have to judge whether the test duration is the same as (i.e., generalization), or shorter/longer than (i.e., discrimination) the standard stimulus (Grondin, 2001; Wearden & Jones, 2013). Reproduction of the standard duration is also used (Kononowicz & van Rijn, 2011; Macar et al., 1999). Participants are said to be making a temporal decision in the prospective timing task (Klapproth, 2008), because the amount of time is the evidence they need to gather to make a decision.

In order to make a temporal decision, the pacemaker-accumulator model assumes the participant compares the current time lapsed with the target, also known as the criterion or referent, time. In S1-S2 tasks this is often the first presented S1 stimulus, while the current time, or test duration, is the S2. The comparison is achieved by some ratio between the S1 and S2 durations (Wearden, 2004). Researchers have linked the processes from the formation of temporal memory to temporal decision making to different ERP components, and in particular, the contingent negative variation (CNV).

General Properties of the CNV

Walter, Cooper, Aldridge, McCallum, and Winter (1964) first identified the CNV as an electrophysiological marker of expectancy. In one condition of this classic study, an initial stimulus (S1) served as a cue for presentation of a second stimulus (S2) that appeared one second later. S2 served as an imperative stimulus that required a button-press response in some trials, but not the others. In another condition, there

was no S2, but participants were asked to estimate a 2 s duration before pressing a button. A slow negative potential ramp with a fronto-central topographical distribution appeared during the S1-S2 period when S2 served as an imperative stimulus and in the 2-s estimation condition only. Thus, this negativity, termed CNV, is only elicited when a contingency was established between two stimuli, such that the cue allows the generation of predictions about the upcoming stimulus and facilitates its processing stages (e.g., Correa et al., 2006; Jepma, Wagenmakers, Band, & Nieuwenhuis, 2008; Seibold, Bausenhart, Rolke, & Ulrich, 2011). This facilitating effect is loosely known as expectation, anticipation, or preparation, and is not limited to the temporal relationship between two stimuli (Los & van den Heuvel, 2001; Weinbach & Henik, 2012). The contingency is also not limited to two discrete stimuli such as a cue and a target (Correa et al., 2006; Macar & Vitton, 1982; Miniussi, Wilding, Coull, & Nobre, 1999; Walter et al., 1964), but also onset-offset of a continuous signal (Campbell, Herzig, & Jashmidi, 2009; Pfeuty, Ragot, & Pouthas, 2003a, 2005, 2008), coincidental timing from stimulus onset to time to contact (Masaki, Sommer, Takasawa, & Yamazaki, 2012), and isochronous stimulus sequences (Pfeuty, Ragot, & Pouthas, 2003b; Praamstra, Kourtis, Kwok, & Oostenveld, 2006). The constituent stimuli can be in the visual, auditory, or tactile domain (e.g., Macar & Vidal, 2003).

Early investigations of the properties of the CNV revealed that it has at least two subcomponents (Figure 2.1). The initial CNV (iCNV) is elicited within about 1s of S1 onset and sometimes peaks within one second. It is modulated by the perceptual properties of the S1 stimulus such as its modality, intensity, and probability (Higuchi, Watanuki, & Yasukouchi, 1997; Kok, 1978; Pfeuty et al., 2008; Rohrbaugh, Syndulko, & Lindsley, 1978, 1979; Scheibe, Schubert, Sommer, & Heekeren, 2009; Scheibe, Ullsperger, Sommer, & Heekeren, 2010; Trillenberg, Verleger, Wascher, Wauschkuhn, & Wessel, 2000). The second subcomponent, the termination CNV (tCNV), usually appears one or two seconds before S2, and increases in negativity as

the S2 onset approaches (Ruchkin, Sutton, Mahaffey, & Glaser, 1986). It is modulated by stimulus anticipation (Damen & Brunia, 1987; van Boxtel & Brunia, 1994), task load (Birbaumer et al., 1990), motor preparation (e.g., motor programming of the response to S2; Ulrich, Leuthold, & Sommer, 1998) and instructions that emphasize response speed (Flores, Digiacomo, Meneres, Trigo, & Gómez, 2009; Loveless & Sanford, 1974; Rohrbaugh & Gaillard, 1983); further evidence suggests that it does not purely reflect motor execution (Brunia, 2003; Damen & Brunia, 1987). If the S1-S2 duration is long enough (> 4 seconds), the two subcomponents often appear as a bimodal, long-lasting CNV (Gibbons & Rammsayer, 2004; Rohrbaugh, Syndulko, & Lindsley, 1976); otherwise, the two components may overlap (Bender, Resch, Weisbrod, & Oelkers-Ax, 2004).

A final third component of CNV was suggested by Macar and Besson (1985) based on a comparison of the CNVs generated in a simple reaction time task, a 4-second foreperiod task, a 4-second temporal production task, and the encoding phase of a 4-second temporal reproduction task. They observed the largest CNV in the temporal reproduction task that could not be fully accounted for by motor preparation to S2. In another experiment, the time course of the CNV elicited during a timing task was also found to differ from the 'classical' CNV, with the former CNV reaching maximal negativity and resolving back to the baseline potential much earlier (Macar & Vitton, 1982; see below). The authors argued that this 'temporal' CNV reflects the temporal and probabilistic linkage between S1 and S2. Consistent with this assertion, using principal component analysis (PCA), Lutzenberger, Elbert, Rockstroh, and Birbaumer (1981) observed a third PC with a latency between the PCs reflecting iCNV and tCNV, although the temporo-spatial manifestation of this PC was quite variable.

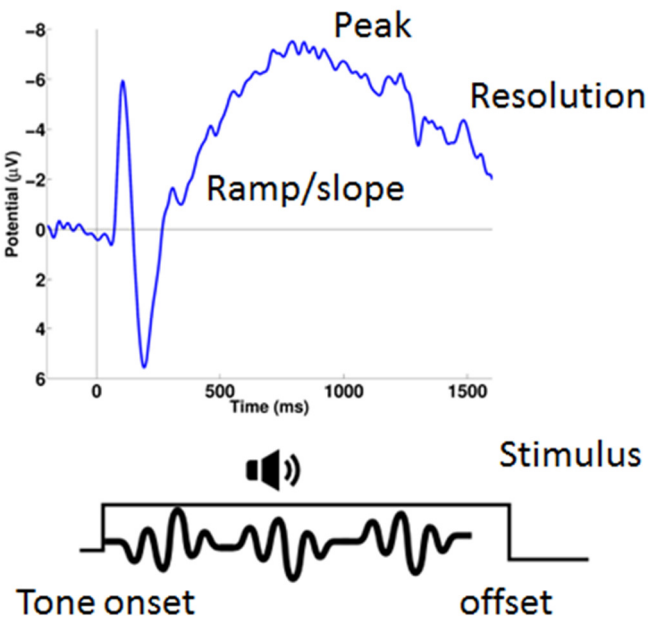


Figure 2.1. An example of the CNV triggered by a continuous tone. After the auditory evoked potentials, a rapid rise in negative voltage lasts for an extended period of time and returns to baseline after peaking.

Neural substrates of the CNV and the time perception network

In the research on time perception, researchers claimed that the CNV reflects the underlying timing mechanisms. A few groups further asserted that these mechanisms are consistent with the pacemaker-accumulator model. This link between the CNV and timing has been established based on the neural origin of the CNV and the characteristics of the CNV time course.

A considerable overlapping has been observed between the CNV neural generators and the neural network thought to subserve interval timing. Not only is the CNV observed when participants encode and compare durations (e.g., Casini & Vidal, 2011; Chen et al., 2010; Coull, Nazarian, & Vidal, 2008; Le Dantec et al., 2007), but its neural substrates are also always implicated in interval timing, as shown with electrophysiological and functional neuroimaging data. On one hand, surface Laplacian ERPs (Macar et al., 1999; Macar & Vidal, 2002), source localizations of EEG and MEG data (a magnetic counterpart of EEG; Ferrandez & Pouthas, 2001;

N'Diaye, Ragot, Garnero, & Pouthas, 2004; Onoda, Suzuki, Nittono, Sakata, & Hori, 2004), and intracranial EEG recordings (e.g., Bareš et al., 2003; Hamano et al., 1997) all show that the Supplementary Motor Area (SMA), the pre-SMA (Kotz & Schwartze, 2011), the right dorsal lateral prefrontal cortex (DLPFC, Coull, Vidal, Nazarian, & Macar, 2004), and posterior perceptual cortices are among the major neural generators of the sensorimotor CNV. On the other hand, fMRI analyses also consistently identify the SMA and DLPFC in sub- and supra-second timing (see Coull & Nobre, 2008; Lewis & Miall, 2003a, 2003b; Penney & Vaitilingam, 2008; Stevens, Kiehl, Pearlson, & Calhoun, 2007; Wiener, Turkeltaub, & Coslett, 2010 for reviews).

The CNV Time Course and Timing Task Performance

Another important support for the CNV-timing relationship comes from the changes in the CNV features caused by manipulating the demand for timing in the experiments. A number of studies have revealed an association between the CNV and prospective time perception performance (e.g., Casini, Macar, & Giard, 1999; McAdam, 1966), although these data patterns may not immediately lend support to any specific timing models (cf. Liu et al., 2013). For example, Ladanyi and Dubrovsky (1985) compared performance and CNVs of participants making verbal estimates of 10 or 20 seconds. Compared to less accurate estimators, the more accurate estimators showed CNVs with smaller amplitude, earlier resolution, a slower ramping to the maximum negativity. More recently, Pfeuty et al. (2008) tested participants' temporal discrimination when stimuli were filled tones and empty intervals demarcated by two brief tones. They found that the CNV amplitude was significantly larger (see Mitsudo, Gagnon, Takeichi, & Grondin, 2012) and performance (accuracy) significantly worse when the intervals were filled (69% correct) as compared to empty (77% correct). However, Gontier et al. (2009) found the opposite pattern that more negative CNV amplitude was associated with higher accuracy in temporal discrimination. A recent experiment by Wiener et al. (2012)

showed stronger causality between the CNV and time perception using rapid transcranial magnetic stimulation (rTMS), which perturbs neural activity by non-invasive application of strong external magnetic fields to the scalp. Participants performed temporal discrimination with and without rTMS applied to the right superior marginal gyrus (SMG). The difference in the mean CNV amplitude (270-470 ms) between rTMS and non-rTMS trials and the difference in an index derived from the proportion of 'longer than standard' responses in rTMS and non-rTMS trials were computed. A positive correlation was found between the two measures, favoring the CNV-timing connection.

Interpreting the CNV-Timing Link with the Pacemaker-Accumulator Model

The CNV-timing association that is most pertinent to the experiments conducted in this dissertation is its interpretation within the framework of the pacemaker-accumulator model (Macar & Vidal, 2004; Macar & Vidal, 2009). As described in Chapter 1 and the beginning of the CNV introduction, the number of pulses stored in an accumulator determines the perceived duration of the event of interest. Comparison of this pulse count with representations of relevant durations held in long-term memory forms the basis of the decision process in most prospective timing tasks (Wearden, 2004). For this model to realize in the human brain, some neural units must act as the accumulator. Their activation should increase over time. Longer intervals are represented by more total clock pulses, which should mean higher final neural activation. Researchers claim that the CNV shows these properties in S1-S2 timing tasks.

CNV generation and neural accumulation. While the debate about the structure of the brain clock is ongoing (Buhusi & Meck, 2005; Ivry & Schlerf, 2008; Mauk & Buonomano, 2004; Meck et al., 2008), the idea that neurons or groups of neurons act as accumulators of incoming neural signals for subsequent processing is not new and is an important one. It has been used extensively to account for

perceptual decision-making (Ratcliff, Philiastides, & Sajda, 2009; Simen, 2012; Zhang, 2012), response competition and inhibition (Burle, Vidal, Tandonnet, & Hasbroucq, 2004), as well as numerical cognition (Meck & Church, 1983; Nieder & Dehaene, 2009). Early investigations of the neural mechanisms responsible for generating the CNV suggest that this slow cortical potential is due to the summation of excitatory post-synaptic potentials at the apical dendrites in deeper cortical layers, an indication of increased cortical excitability (Birbaumer et al., 1990; Rockstroh, Müller, Wagner, Cohen, & Elbert, 1993). The neurons that generate the CNV may show ramp-like firing patterns, such that they increase their firing rate as time passes and are capable of adjusting it according to the temporal relationship between the cue and the imperative stimulus (Durstewitz, 2003; Komura et al., 2001; Mita, Mushiake, Shima, Matsuzaka, & Tanji, 2009; Reutimann, Yakovlev, Fusi, & Senn, 2004). The ramping negative potential of the CNV may then be a result of an accumulation process due to spreading activation or signal integration (König, Engel, & Singer, 1996) of these 'climbing' neural activities in the medial frontal brain areas (Macar et al., 1999; Macar & Vidal, 2004; Macar & Vidal, 2009; Macar, Coull, & Vidal, 2006; Meck et al., 2008; Pfeuty et al., 2005; Simen, Balci, deSouza, Cohen, & Holmes, 2011a, 2011b).

CNV amplitude and the accumulator. The hypothesis that the CNV amplitude, an indication of the level of cortical activation, reflects a neural accumulator at work during duration estimation has received some support. In a landmark paper, Macar et al. (1999) showed a relationship between CNV amplitude, as determined from a surface Laplacian computation, and the perceived duration of the 2500 ms target interval in a temporal reproduction task. The authors assigned the reproduction trials to one of three categories based on accuracy (2600-2800 ms; 2400-2600 ms; 2200-2400 ms) and then generated response locked CNVs for each category by participant. Comparison of the grand average waveforms of the three groups of

trials indicated that the CNV amplitude became less negative as the produced intervals decreased, even though the participants were attempting to reproduce the same 2500 ms target duration in all cases. In a subsequent experiment, Macar and Vidal (2002) further showed that the amplitude of the surface Laplacian CNV did not reflect learning or updating of the temporal memory of the target duration (Condition 1), because the difference in the CNV amplitude after trial classifications was not observed when feedback about performance was provided (same as the 1999 study), but the participants were not given any practice to acquire the standard duration (different from the 1999 study). Instead, the differences in the CNV amplitude only emerged when trial classification was based on individuals' mean reproduced duration and no accuracy feedback was given so that the mean reflected participants' preferred/biased representation of the standard duration (Condition 2). This performance-dependent relationship led the authors to conclude that the CNV reflects a consolidated representation of the standard duration. The importance of memory consolidation in determining the CNV was also suggested by Mochizuki and colleagues (Mochizuki, Takeuchi, Masaki, Takasawa, & Yamazaki, 2005), who varied the retention period (3000 or 9000 ms) between encoding and reproduction of a 2700 or 3000 ms stimulus. The CNV during the reproduction phase was larger for the 9000 ms retention interval, which the authors attributed to a stronger need to reactivate the decayed memory of the target duration when the retention interval was longer.

Using a temporal discrimination task with much shorter intervals (500 ms on average), Bendixen, Grimm, and Schröger (2005) replicated and extended the amplitude effect of Macar et al. (1999). They compared the grand average onset-locked CNV of trials that received a 'short' response to those that received a 'long' response, based on data from probe durations showing maximum response variability

(480 and 520ms). The N100 and CNV amplitudes were more negative when the response was 'long', in line with the pacemaker-accumulator hypothesis.

However, Macar and Vidal (2003) failed to replicate the association between CNV amplitude and perceived duration/temporal performance when untrained participants were tested on a temporal discrimination task using intervals of about two seconds. More recently, Kononowicz and van Rijn (2011) also failed to find the association in a replication of the paradigm used by Macar et al. (1999). Instead, these authors found evidence for a habituation effect on the CNV amplitude across the experimental session. In a related review paper, they further argued that the polarity of the difference in CNV amplitude reported in previous studies is not fully compatible with the pacemaker-accumulator hypothesis (Tipples, Brattan, & Johnston, 2013; van Rijn, Kononowicz, Meck, Ng, & Penney, 2011). Several other experiments using temporal discrimination, or implicit timing tasks with sub- and supra-second durations with untrained participants also failed to find a difference in the CNV amplitude as a function of the duration of the intervals (Elbert, Ulrich, Rockstroh, & Lutzenberger, 1991; Gibbons & Rammsayer, 2004; Pfeuty et al., 2005).

To summarize, multiple studies have demonstrated a consistent relationship between CNV amplitude and performance in many timing tasks. Researchers propose that this shows that the CNV indexes the consolidated temporal memory of the standard duration, which results from a pacemaker-accumulator process. However, interpreting these results as evidence for the pacemaker-accumulator model of time perception appears unwarranted given the sum total of available evidence.

CNV peak latency and slope and temporal decision making. The initial ramping and subsequent resolution of the CNV amplitude are also claimed to reflect the accumulation and the memory representation of the target duration, respectively. For the initial ramp, researchers have drawn attention to the resemblance between the

CNV's gradual increase in negativity and climbing neuron firing patterns (Durstewitz, 2003, 2004; Pfeuty et al., 2005; Simen et al., 2011a, 2011b). Pfeuty et al. (2005) proposed that the comparison between the memorized standard and the count in the accumulator has a fixed criterion regardless of the range of durations that are in question. The encoding and differentiation of durations is achieved by adjusting how rapidly the climbing neural activity reaches this criterion. Hence, the CNV ramp should vary depending on the durations used. This ramp difference was supported in Pfeuty et al.'s (2005) temporal discrimination study using two experimental blocks that employed different standard durations (600 and 794 ms): the initial CNV slope was steeper in the block with the short standard, with the CNV maximal negative amplitude being the same between blocks, implying an identical criterion (Loveless & Sanford, 1974; Ruchkin et al., 1986).

Besides the CNV ramp, the pacemaker-accumulator hypothesis also predicts that its amplitude should resolve before the end of the test stimulus when the test duration is longer than the standard, because once the comparison criterion is reached, a temporal decision can be made without the need of further pulse accumulation. The amplitude resolution thus marks the moment of decision-making in interval timing (Macar & Vidal, 2003; Pfeuty et al., 2005; Tarantino et al., 2010). Several research groups (e.g., Ladanyi & Dubrovsky, 1985; Macar & Vitton, 1982; Ruchkin, McCalley, & Glaser, 1977) noted that a critical difference between the CNV induced by sensorimotor manipulations and the CNV induced by changes in time is the early amplitude resolution in the latter case. For example, using relatively long intervals (e.g., > 5 seconds) in a temporal discrimination task, Macar and Vitton (1982) observed that the CNVs corresponding to the standard (SI) and target intervals (TI) resolved before the end of the intervals, while the SI-TI delay (3 seconds) and the delay between TI termination and response (3 seconds) showed a more 'classic' expectancy CNV that did not resolve until the end of the specific interval. It is

purported that a positive decision-making or motor programming component, such as the P300 (Birbaumer & Elbert, 1988; Deecke & Lang, 1988; Donchin & Smith, 1970; Kok, 1978) and the Late Positive Component of time (LPCt; Paul et al., 2011; Paul, Le Dantec, Bernard, Lalonde, & Rebaï, 2003; Tarantino et al., 2010) may be superimposed on the CNV (Ruchkin et al., 1977).

Macar and Vidal (2003) showed a more intimate relationship between the latency of the CNV peak/ resolution and the memorized standard using both visual and tactile temporal generalization tasks. They showed that the CNV peaked at the memorized target duration (2000ms) rather than at the end of the probe duration (2500 or 3100ms). Pfeuty et al. (2003b) obtained similar results with a S1-S2 duration comparison task. During S2, the CNV reached its negative peak at the S1 target duration (700ms) at left hemisphere and medial frontal electrode locations, while at right hemisphere frontal electrode sites the CNV peaked at the end of S2. The authors suggested that the distinct CNV profiles at the right and left hemisphere electrodes reflected separate memory representations for the S1 target duration and the elapsing S2 duration. Furthermore, there was a correlation between the CNV peak latency and the subjective standard derived from the generalization gradient. In a subsequent S1-S2 temporal discrimination experiment (Pfeuty et al., 2005), the authors showed that given the same S2 probe duration (794 ms), the peak latency of the CNV corresponded to the S1 target duration (600 vs. 794 ms). Pfeuty et al. (2008) then compared the CNV elicited during the timing of filled and empty auditory signals. A filled duration is the amount of time of a continuous signal, while an empty duration is the amount of time demarcated by two brief auditory pips. The results showed that the CNV of the filled signal peaked at the standard duration (600 ms) and maintained this peak amplitude for a brief period of time before decreasing, while the CNV of the empty signal increased in negativity after reaching 600 ms. The authors attributed this

common sensitivity to the standard duration, but different CNV profile to the differences in the sensory differences between the two signals.

This CNV resolution is also observed in timing tasks other than S1-S2 prospective timing tasks. Praamstra et al. (2006) replicated the peak latency relation with the target duration in an implicit motor timing task. In this task, participants pressed one of two keys depending on whether an arrow pointed to the left or the right. Each trial comprised a short sequence of cues, each presented isochronously (2000 ms) with the exception of the final cue. A CNV occurred between successive cues, but when the final cue was presented late (2500 ms), the CNV peaked at the expected inter-stimulus interval (2000 ms) and then began to resolve. Mento, Tarantino, Sarlo, and Bisiacchi (2013) went one step further to omit any overt motor responses by using an oddball task with a visual stimulus of 1500 ms as the frequent standard stimulus (70%) and 2500 ms and 3000 ms (15% each) as the rare deviants. Participants were not given any instruction about timing the stimuli or responding to them. Still, the CNVs of the deviants peaked at about the standard duration, suggesting that participants constructed predictions about the temporal information available in the task, as reflected by the oddball CNV. The occurrence of this peak despite the omission of overt responses also implies that the CNV resolution observed in aforementioned studies is not simply due to motor potentials, but a true neural response to anticipation (cf. Brunia, 1999).

To summarize, the CNV triggered in timing tasks seems to show an earlier resolution than the sensorimotor CNV. Limiting to timing experiments, some studies have reported a non-specific early CNV resolution that is performance-dependent, while some have found the resolution to be tied to the memorized standard, indicating the end of temporal information accumulation. On the other hand, a few studies also looked at the ramp of the CNV potential and suggested it reflects an accumulation process resembling the climbing neural activity. Overall, in contrast to the findings

for the amplitude of the CNV, those for the peak latency and slope of the CNV as reflecting the end of the remembered standard duration appear to be reasonably consistent.

Time Estimation in the Duration Bisection Task

Since the evidence obtained with S1-S2 paradigms to support the pacemaker-accumulator model is mixed, examination of this CNV-timing association using a third kind of task may provide clarification. To this end, the duration bisection task was adopted.

The duration bisection task is a task with simple instructions and can be used across species to study the universality of time perception (Church & Deluty, 1977; Penney, Gibbon, & Meck, 2008). For example, it was used to investigate whether animals represent time (and other properties) on a logarithmic or linear scale (Raslear, 1982). The task was later adapted to study human timing (Wearden, 1991). In a typical duration bisection experiment with humans (Figure 2.2), participants are asked to classify probe (or test) durations as closer to either the short or the long anchor duration (e.g., 2 vs. 8 s) learned in training. The probe durations usually comprise either a geometric or an arithmetic series that includes the short and long anchors as well as intermediate durations. The bisection task is so called because a range of test durations are compressed into two categories that invite different responses. The resultant response function, the proportion of 'Long' response (p('long')) as a function of probe duration, is ogive-shaped with a perceptual boundary at some central tendency of the stimuli, the signature of categorical perception (Penney et al., 2008).

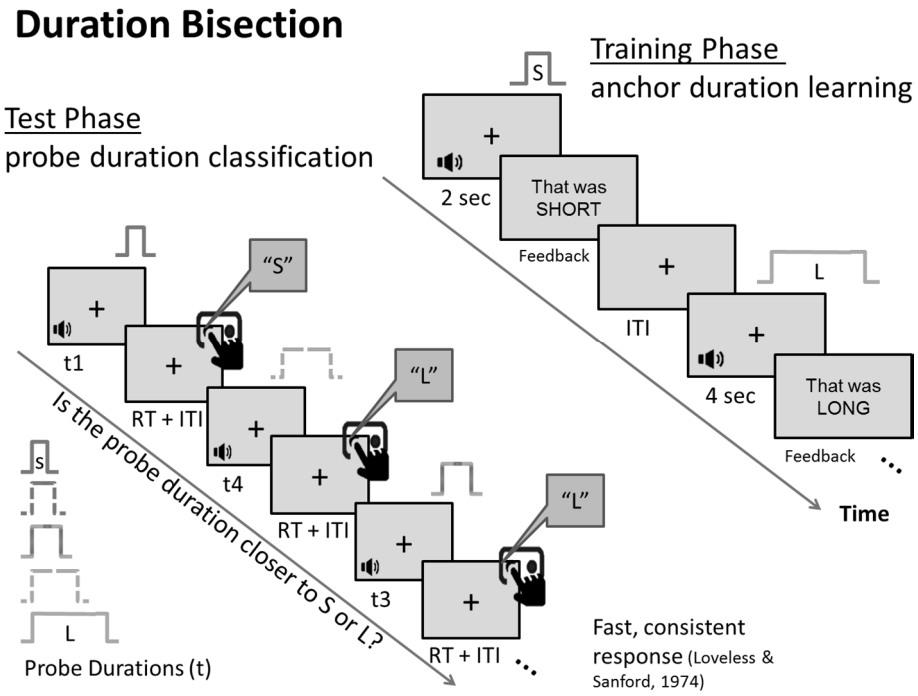


Figure 2.2. Demonstating the bisection task. Conventional version starts with the learning/training phase (right), in which participants have to learn two anchor durations. In the testing phase (left), probe durations equal to the anchors or with intermediate durations are presented one by one. Participants make a similarity judgment at the end of the probe tones by a motor response.

The criterion time in the bisection task. The point of subjective equality (PSE), the difference limen (DL), and the Weber fraction (WF) can be obtained from the participant's psychometric response function (Gibbon, 1981). These measures are useful for the study of the perceptual and cognitive factors that can influence subjective perception of time (e.g., Penney et al., 2000; Vicario, 2011). The DL and WF are computed from the steepness of the ogive function and index temporal sensitivity like other timing tasks. This sensitivity is sometimes called endogenous temporal uncertainty (Balci et al., 2011), representing the temporal precision an individual is capable of. The PSE is calculated as the duration with a p('long') of .5. In timing tasks with a S1-S2 design, the PSE is an index of the participant's subjective estimation of the standard duration as S1, which is also the criterion time for the temporal decision making. The PSE may be interpreted in a similar fashion in the bisection task, whose shifting implies changes in subjective estimation of time

(e.g., Ortega, Lopez, & Church, 2009; Spínola, Machado, de Carvalho, & Tonneau, 2013). However, this 'standard duration' located at the PSE is never explicitly learned in the bisection task: it either lies close to the geometric mean (GM) or arithmetic mean of the two anchors (AM), mid-way between the two anchor durations participants were instructed to learn (Kopec & Brody, 2010).

While it is believed that the memories of the two anchors are formed during the learning phase, no direct evidence has yet confirmed whether a temporal memory is formed for the bisection criterion at the PSE. Nevertheless, there is support from behavioral data that this is the case. Even in a design as simple as an S1-S2 paradigm, multiple pieces of temporal information are present: S1, S2, the inter-stimulus interval (ISI), and intertribal interval (ITI), and the total duration of a trial. Despite this proximity between the two major durations of interest, some evidence indicates that the trial referent is not used veridically. For instance, an early model suggested that the test duration is compared against the time from trial onset to the S2 onset and no memory component is included in this kind of temporal discrimination (Eisler, 1975). There is also the time-order error (TOE), referring to the tendency for participants to perceive the S2 to be longer than S1 (and sometimes vice versa; Allan, 1979; Zakay, 1990), with occasional modulation by the ISI (e.g., Schab & Crowder, 1988), indicating temporal memory decay and interference (Wearden & Ferrara, 1993). In addition, when different standard durations are intermixed in the same experimental block, participants respond as if they have merged the two standard durations to form a new criterion time (Gu & Meck, 2011).

Research shows that humans unconsciously extract statistical properties of the stimulus and construct central tendencies for making comparisons, including time (Ariely & Zakay, 2001; Balci & Gallistel, 2006). Various studies showed that mental arithmetic on time is possible (van Rijn & Taatgen, 2008), and participants adapt their temporal memories in face of changing temporal experiences (Jazayeri & Shadlen,

2010; Taatgen & van Rijn, 2011), as a means to balance between temporal uncertainty and accuracy (Balci et al., 2011 Gu, Jurkowski, Lake, Malapani, & Meck, in press; Gu & Meck, 2011). Vierordt's Law (Lejeune & Wearden, 2009), which refers to the overestimation of short durations but underestimation of long durations, may be the result of generation of an internal criterion through memory mixing (Gu & Meck, 2011; also see Chapter 5). In memory mixing, durations experienced previously in the same session are all pooled together to form the distribution of the temporal memory of the standard, from which a sample is drawn when a temporal decision needs to be made. Consistent with these observations, Klapproth and Müller (2008) showed that participants underestimated the standard duration in a temporal generalization task when they were instructed to respond as quickly as possible, even if the test duration presentation was not over. They posited that since the test durations longer than the memorized standard were truncated in the former, any updating of the bisection criterion would rely on a smaller duration range, leading to the shortening of the criterion; this occurred despite refreshed presentation of the veridical standard as S1 in each trial (see also Klapproth & Wearden, 2011).

If the trial standards are not used veridically, but subject to assimilation with previous temporal experiences even in the S1-S2 design, then we might also expect this to occur in the duration bisection task. In fact, there is some evidence that participants use a central tendency for temporal decision in duration bisection. For example, participants' performance was remarkably similar in the conventional bisection task as well as in the partition task, which is identical to the bisection task in all aspects except that there is no explicit learning of the two anchors at all (e.g., Droit-Volet & Rattat, 2007). Intuitively, participants can successfully bisect the durations by forming a single criterion representation at some mid-point of the shortest and longest probe durations. Balci and Gallistel (2006) asked participants to perform a bisection task with anchor durations of 2 and 4 seconds. They used

likelihood ratios to compare different bisection models and showed that models with ratios between the probe duration and a central tendency parameter (i.e., probe/AM or probe/GM) are much more likely than a model requiring ratios between the probe duration and the duration range (i.e., [probe-S]/[L-S]). This reliance on a central tendency of all available temporal information was also demonstrated with a modified version of the bisection task by Allan and Gerhardt (2001). Participants were asked to classify the probe duration based on the 'roving' anchor durations: a new pair of anchors were presented at the beginning of each bisection trial like a S1-S2 design; several different sets of anchor and probe durations were thus used in one experimental session. Despite the provision of trial anchors, the participants responded as if they had taken the whole range of durations used in the same session into consideration (cf. Rodríguez-Gironés & Kacelnik, 2001).

An intriguing experimental design further emphasized the fact that the temporal decision in the bisection task cannot be solely relying on the two anchor representations (e.g., Kopec & Brody, 2010), but also those of the probes, as demonstrated in the bisection experiments by Brown, McCormack, Smith, and Stewart (2005) using durations between 200 and 900 ms (see also Wearden & Ferrara, 1995). They used probe duration series that were either geometrically spaced (equal ratio *n* between successive durations), hyper-geometrically spaced (increasing ratio), or reversed-geometrically spaced (equal ratio *1/n*), and found that the PSE shifted according to the distribution so that it stayed close to the 'center of mass' (Ryan, 2011). This sensitivity of the PSE to the temporal relations between probes is consistent with the memory mixing hypothesis (Gu & Meck, 2011; Taatgen & van Rijn, 2011).

This is not to say the initial learning of the two anchors is redundant to the bisection criterion given the more intensive and recent interference from the probe durations. The learning of anchor durations at the beginning of the bisection task may

establish a clear duration range on which the central tendency is based (Allan & Gerhardt, 2001; Allan, 2002a). The indispensable role of the anchor durations was exemplified in a developmental study by Droit-Volet and Rattat (2007). Three groups of children and adults were tested on the typical bisection task (prior anchor learning) and partition task (no anchor learning). Five-year-old children, although not adults, showed improved temporal performance if anchor durations were presented prior to the bisection trials. These findings suggest that the prior anchor presentations help participants establish the bisection criterion.

To recap this chapter, we provided a simplified introduction to the neurophysiology of EEG and ERP. Researchers argue that the CNV reflects timing mechanisms because CNV amplitude and peak latency/ amplitude resolution showed performance-dependent properties in timing tasks. Some further asserted that it supports the pacemaker-accumulator model of timing. We then introduced the duration bisection task as a useful task to validate the CNV-timing linkage usually found in S1-S2 paradigms. Specifically, if the CNV reflects the pacemaker-accumulator model of timing, we expect the CNV time course to be consistent with the predictions given by this model, namely 1) CNV negativity increases as a function of perceived time (Macar et al., 1999; Macar & Vidal, 2002), 2a) CNV ramp is more rapid when the target duration is shorter, so that 2b) the earlier the maximal CNV negativity, which should be similar regardless of the target duration, is reached, the shorter the target duration (Pfeuty et al., 2005), and 3) the CNV peak latency or time of resolution reflects the end of target duration, because enough temporal information is accumulated for a certain temporal decision (Macar & Vidal, 2003). If these patterns cannot be observed, then it suggests that this ERP component does not uniquely provide support to any specific timing mechanisms, but instead reflects either processes that are dependent on the clock, but not the clock *per se* (van Rijn et

al., 2011), or non-clock processes that are nevertheless essential to optimal bisection performance (e.g., Livesey, Wall, & Smith, 2007).

Chapter 3 Experiment 1 Study of the Duration Bisection Task Using the CNV

While being a popular prospective timing task, the duration bisection task has not been used in conjunction with EEG or other brain imaging methods very often. In experiment 1, this task was used to verify whether the CNV reflects a pacemaker-accumulator process.

According to the timing hypotheses of the CNV, a consolidated memory of the criterion/standard duration is required (cf. Macar & Vidal, 2002) for the CNV amplitude to reflect subjective duration. This consolidation may be readily observed in S1-S2 timing tasks because the standard duration is refreshed during every trial to resist deviation due to memory decay and interference (Buhusi & Meck, 2006; Wearden & Ferrara, 1993). As discussed in Chapter 2, participants also can bisect the interval range in the partition task, in which no anchors are learned. This suggests that memories in addition to the anchor memories are used in the bisection decision. This bisection criterion was also shown to be quite stable. For example, Gamache and Grondin (2010, Experiment 2) studied the modality effect in subjective duration estimation (i.e., auditory durations are judged longer than equivalent visual durations, see Chapter 5) by asking participants to finish one block of a bisection task with durations in one modality (e.g., auditory) and nine subsequent blocks with durations in the other modality (e.g., visual). Participants indicated their perceived duration by bisecting a straight line. Instead of an abrupt change in the line length after switching from one modality to another, as would be expected if participants formed no memory from the first block, it took five blocks of seven trials for the new criterion to settle (due to memory mixing). This gradual shift is also consistent with pharmacological manipulations of the temporal reference memory in animals (Meck, 1996). Furthermore, if the two different duration ranges used in the same session are different enough, participants can maintain two different criteria and perform the two bisection tasks quite satisfactorily, despite occasional interference between the two

(Spínola et al., 2013; Trujano & Zamora, 2013). This is unlikely if participants rely only on temporal information from very recent trials. Therefore, bisection performance is likely to be dependent on relatively stable bisection criterion shaped by recent temporal experience, but not completely driven by probe durations immediately before a given trial, as in S1-S2 tasks.

In the previous chapter, we reviewed the putative role of the CNV as a marker of interval timing, especially with the pacemaker-accumulator model in mind. Specifically, the CNV at medial frontal electrode sites should reach its negative peak when elapsed time matches a remembered target duration, and begin to resolve when the categorization decision is made. In the case of duration bisection, this means that if the critical information is whether the currently elapsing duration has exceeded the memory representation of the criterion time, then the CNV should peak and resolve when the current duration exceeds the criterion time, approximated by the PSE or the central tendency of the probe durations (e.g., the geometric mean, GM, Allan & Gerhardt, 2001). We also corroborated the electrophysiological data with behavioral measures, namely the PSE and the response times (see Analyses) to show that temporal decision is indeed more difficult near the PSE, as further behavioral support of the bisection criterion.

The pacemaker-accumulator hypothesis proposes further that the CNV amplitude reflects temporal memory and is a function of perceived duration: Longer the duration, more pulses are accumulated, thus higher neural activation and more negative CNV amplitude. In the current experiment, we examined the variation in subjective time within-subjects by studying the ERPs generated from intermediate probes that are close to the PSE, but categorized differently. To this end, similar to Macar et al. (1999), Bendixen et al. (2005), and Pfeuty et al. (2005), trials from these probes were grouped and averaged according to the response each trial received, and their ERPs compared. We expected the CNV of trials classified as long to be more

negative than that of trials classified as short, among other possible differences such as the resolution time.

Tipples et al. (2013) studied time perception in humans with fMRI using the duration bisection task with durations between 400 and 1600 ms and found that participants' degree of overestimation of time (shortening of PSE) was positively correlated with activity in the right inferior frontal gyrus and SMA. Hence, we assumed that if the pacemaker-accumulator clock times duration by adjusting the rate of the climbing activity (Simen et al., 2013), then a correlation between the CNV ramp and participants' PSE should obtain.

To conclude, two of the three hypotheses stated at the end of Chapter 2 were examined in Experiment 1. First, the CNV peak latency or resolution should match with the bisection criterion, PSE. Second, variation in subjective time should be reflected in the CNV amplitude and/or CNV ramp.

Method

Participants

Seventeen students at the National University of Singapore (aged 19-30 years, nine females) gave informed consent and took part in a one-session duration bisection experiment. All participants had normal or corrected-to-normal vision and normal hearing. All but one were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971; http://www.psy.otago.ac.nz/miller/Software.htm).They were naïve to the experimental hypotheses and were reimbursed for their participation at a rate of SGD10/hour.

Stimuli

An auditory or visual signal served as the 'carrier' (Wackermann & Ehm, 2006) of the various probe durations. Auditory probe durations were employed in all three experiments. Stimuli comprised seven 440 Hz sinusoidal tones, with 10 ms rise

and fall times, played over stereo headphones at a comfortable level. A total of seven logarithmically distributed probe durations (t) were used in all blocks (800, 1008, 1270, 1600, 2016, 2540, and 3200 ms), with 800 ms and 3200 ms being the short (S) and long anchors (L), respectively.

Procedure

An experimental session typically lasted for 1.5 to 2 hours including EEG set-up and clean-up time. Each participant completed two test blocks. The participant's ongoing EEG, response choices and response times (RT) were collected during each experimental session.

The duration bisection paradigm (Gibbon, 1981) was implemented in E-Prime 1.2 (Psychology Software Tools, Inc., Pittsburgh, PA). At the beginning of each block, the two anchor durations (S and L) were presented to the participants five times each in a randomized order. Feedback was provided on the computer screen after each stimulus presentation ("That was the Short/Long duration"). The test phase commenced 3000 ms after the end of anchor training, starting with the on-screen text 'Ready, the test phase is starting'. In this phase, feedback was not provided to allow individual differences in subjective time (Macar & Vidal, 2002). The inter-trial interval (ITI) was a combination of the participant's response time (RT) and a random duration drawn from a uniform distribution between 1000 and 2000 ms. The time window for responding was 2000 ms. Trial order within a block was pseudo-randomized such that no consecutive probe durations were the same. Each probe was repeated 28 times within a block (i.e., a total of 56 trials per probe).

Participants sat in a dim, sound-attenuated room about 100 cm in front of a 20-inch CRT computer screen with a screen resolution of 1024 by 768 pixels and a vertical refresh rate of 60 Hz. Responses were collected via a response box (Cedrus). Participants positioned their arms comfortably so that their left and right index fingers

were always touching the two keys on the response box. They were told that they had to attend to a series of tones and press on the appropriate response box key to indicate whether they thought the tone duration was more similar to S or L during the test phase. They were told to respond only when the tone terminated in a quick, but not hasty fashion, similar to the 'normal' instruction given by Loveless and Sanford (1974), who told their participants to strike a balance between speed and accuracy. Response key assignment was counterbalanced across participants. Counting and tapping was prohibited. Rattat and Droit-Volet (2012) reported that verbal instruction is effective in preventing counting in timing tasks.

Scalp EEG Recording Set Up

EEG was recorded with Ag/AgCl electrodes using a Biosemi ActiveTwo system. Sixty-six electrodes (mastoids included), mounted in an elastic cap according to the 10-20 system, were placed on the scalp, grounded and referenced to the active electrodes CMS and DRL. Electrooculogram (EOG) was recorded from electrodes positioned at the outer canthus of the right eye and just above and below the left eye. One electrode was placed at the nose for offline rereferencing. Data was sampled at 2048 Hz from DC to 410 (-3dB) Hz, and downsampled to 256 Hz offline.

Participants were asked to relax and blink naturally throughout the experimental sessions, but they were also warned about the undesirable consequences on the data due to artifacts and were encouraged to reduce artifact occurrence as much as possible (Picton et al., 2000).

All EEG recordings were processed offline using the MATLAB toolbox EEGLAB (Delorme & Makeig, 2004), separately for each participant. The data was first band-pass filtered between 0.1 and 32 Hz using the filtering function in ERPLAB (erpinfo.org/erplab), an EEGLAB plug-in. The high pass filter chosen was used in previous CNV studies (Gontier et al., 2007, 2009; Lindbergh & Kieffaber, 2013; Paul

et al., 2011; Tarantino et al., 2010) and offers a balanced treatment between the signals of interest and slow artifacts (Acunzo, MacKenzie, & van Rossum, 2012; Lopes da Silva, 2010; Widmann & Schröger, 2012). The filtered data were visually inspected to remove rare artifacts and bad channels, and then epoched from 200 ms before tone onset to 3500 ms after tone onset. This artifact-reduced data was then subjected to Independent Component Analysis (ICA, Stone, 2002) to isolate artifact ICs (e.g., eye blinks, ECG, and eye/ muscle movements). Eyeblink, eye movement and other artifact ICs were discarded, and the remaining ICs were back projected to the electrode space to obtain clean EEG epochs. The baseline of the EEG epochs began at 200ms pre-stimulus onset. Subject average and grand average ERPs were generated for each electrode site and experimental condition.

Analyses

Data from five participants included too many ocular artifacts and were discarded in the subsequent analyses. Inspection of response functions suggested that their bisection performance was not different from the retained participants. In ANOVA analyses that included within-subject factors with degrees of freedom larger than one, violation of sphericity was Greenhouse-Geisser adjusted. Effect sizes were expressed with the Generalized Eta Squared (ges; Olejnik & Algina, 2003).

Psychometric functions. The psychometric function was generated for each participant by plotting p('long') against probe duration. Given the evidence supporting the existence of an internal criterion in categorical perception (e.g., Balci & Gallistel, 2006), we chose the Pseudo-logistic model (PLM) proposed by Killeen, Fetterman, and Bizo (1997) to fit the psychometric functions. It assumes that participants use the anchors to construct a bisection criterion and use it to guide temporal judgment with respect to the probe durations. Therefore, the model comprises one parameter for the criterion (the PSE), and three for scalar and non-scalar temporal variability. If scalar variability is assumed to dominate, the three

variability parameters can be combined in one index of temporal variability, γ (e.g., Allan, 2002a, 2002b). The model provides an excellent fit to both animal and human duration bisection data, and unifies the temporal decision making in the bisection task with the single-standard, S1-S2 timing tasks (Wearden, 2004). The PLM with two parameters (PSE and γ) was fitted to the classification data of each participant. Fitting was optimized by the nonlinear minimization of residual sum of squares used in the fminsearch function of MATLAB (EzyFit, www.fast.u-psud.fr/ezyfit/).

The PSE, DL, and WF were then obtained from the PLM fit for each participant. The DL was calculated by subtracting the interpolated duration with p('long') = .25 from the duration with p('long') = .75 and dividing the result by two. The WF, an index of temporal sensitivity adjusted for the criterion duration, was computed by dividing DL by PSE. While γ in the PLM is equivalent to WF, we opted for the more traditional WF. In fact, the two indices were almost perfectly correlated in all experiments (all *r*s > .97). The value of the WF served as an indicator of whether the participants performed the bisection task with reasonable precision (Kopec & Brody, 2010).

Response times (RT). Besides the psychometric parameters, RT is also informative (e.g., Droit-Volet, 2010; Gu & Meck, 2011). For instance, Gu and Meck (2011) used it to understand the memory mixing effect in a temporal discrimination task when two standard durations (600 and 1000 ms) were tested in the same block. They interpreted the RT as an indicator of the difficulty of the decision. RT can also reveal a participant's decision confidence (Zakay & Tuvia, 1998). We expected participants to show lower confidence and longer RTs when the probe duration was closest to the PSE, if the PSE is the decision criterion. We argue that participants were more likely to be less confident in these trials since the output at the comparison stage did not allow them to reach a clear decision about which response to give (Balci et al., 2011).

According to Loveless and Sanford (1974), the normal instructions lead to performance more similar to a speed instruction than an accuracy instruction, we expected the RT distributions to be well-behaved. In other words, for probe durations that are considerably shorter than the PSE, the response time measured from the offset of the probe resembles a simple reaction time trial; for probe durations that are reasonably longer than the PSE, the response time to the offset resembles a foreperiod trial, as participants can reorient their attention when they realize the offset has yet to come (Coull, Frith, Büchel, & Nobre, 2000). In both cases, we expect the RT distribution of each probe to be positively skewed (van Zandt, 2000), making the use of mean RT as the dependent variable less desirable. Figure 3.1 shows the RT of each probe from one representative participant.

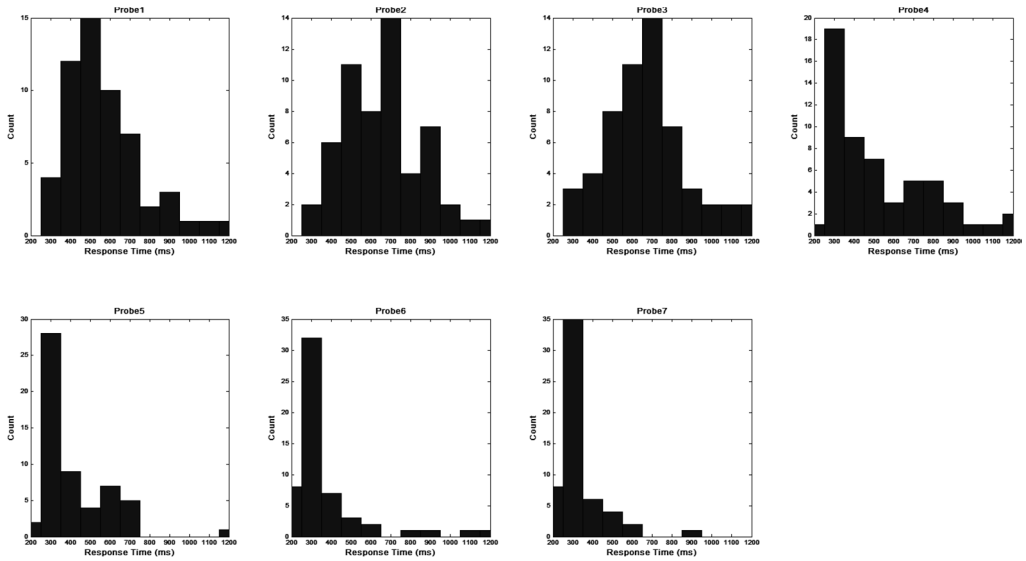


Figure 3.1. Histograms of trial RTs of each probe from a representative participant.

As seen in Figure 3.1, the trial RT distributions across probe durations changed shapes. Thus, fitting appropriate distributions to the RT data allows a more refined depiction of RTs (e.g., Balota & Yap, 2011). A reasonable choice is the ex-Gaussian distribution. It is the convolution between a normal distribution and an exponential distribution, and is fully described by three parameters. *Mu* and *Sigma* describe the mean and standard deviation of the normal distribution component, respectively. *Tau* describes the mean of the exponential component. It describes the

central tendency and variability of very long RTs, which indicates extremes in performance. In general, the ex-Gaussian fit is a good option if no specific theory regarding the underlying distribution of the RT data is made (van Zandt, 2000). While caution should be paid when assigning unique cognitive functions to each ex-Gaussian parameter (Matzke & Wagenmakers, 2009), *Tau* has been suggested to reflect decision processes and attentional lapses, while *Mu* reflects residual processes such as stimulus encoding and motor execution (Leth-Steensen, Elbaz, & Douglas, 2000; Rotello & Zeng, 2008). *Tau* has also been found to be associated with executive functions (McAuley, Yap, Christ, & White, 2006).

The ex-Gaussian parameters were subjected to further analyses. One potential caveat of ex-Gaussian fitting in the current experiments was the limited number of trials for the fitting, which equals the number of trials for each probe duration (56 in Experiment 1, 90 in Experiment 2, 42 or 28 in Experiment 3). We circumvented this issue by first approximating the shape of the RT distribution using a Gaussian kernel with default settings (but limited to be non-zero) in MATLAB (van Zandt, 2000) and obtaining the estimated probability density function (PDF) of the RT of a given probe duration. Then 10,000 trial RTs were randomly sampled from the PDF. Ex-Gaussian fitting was performed on these RTs. This ex-Gaussian fitting yielded similar results as the fitting with the sample RTs and is reported in this dissertation. All the fitting was done using a published fitting routine in MATLAB (Lacouture & Cousineau, 2008).

EEG/ERP analyses. While data from FCz has typically been the focus of CNV analyses (Macar et al., 1999; Pfeuty et al., 2003a, 2003b), here data from FCz and five adjacent electrodes (FC1, FC2, C1, C2, and Cz) were averaged to provide a better signal to noise ratio (cf. Wiener et al., 2012). To further confirm the presence of the CNV component, current source density (CSD) was computed using the CSD toolbox (Kayser, 2009; Kayser & Tenke, 2003) based on the spherical spline algorithm derived by Perrin, Pernier, Bertrand, and Echallier (1989). CSD estimates

the second spatial derivative of the scalp potentials, similar to what is done with the Surface Laplacian (Pizzagalli, 2007). For the CSD computed here, previously validated default values were used, i.e., the order of the Legendre polynomial (n) was 50, the flexibility of the spline (m) was set to 4, and the smoothing parameter (lambda) for the spline interpolation was 10^{-5} (Tenke et al., 1998). Each EEG epoch was first CSD transformed, baseline corrected, and then averaged.

The boundaries of the time windows of each ERP component were determined using the Global Field Power (GFP, Lehmann & Skrandies, 1980) of the ERPs. GFP is computed as the standard deviation of the ERPs of all electrodes at each time point. High GFP value indicates stable configuration of the underlying neural generators. Transitions between ERP components were characterized by small GFP values (Murray, Brunet, & Michel, 2008). The latencies of the transitions between N100 (N1), P200 (P2), and CNV were obtained.

Changes in the CNV time course were investigated by considering the slope of the CNV, i.e., changes in CNV amplitude per unit time (μV/ms). The slopes were obtained by ordinary least squares regression of the CNV amplitude on the time index, based on the subject average ERPs used for the given analysis. Slopes were checked for their direction using one-sample *t*-tests against zero, and compared between conditions or time windows using paired-sample *t*-tests.

Partial Least Squares Correlation (PLSC). Since the slow wave has a wide spread topographical distribution and long lasting time course, we avoided averaging across a large number of electrodes or long time windows by using a multivariate analysis (McIntosh & Mišić, 2013). Partial least squares correlation (PLSC, Krishnan, Williams, McIntosh, & Abdi, 2011; McIntosh & Lobaugh, 2004) extracts spatiotemporal patterns and generates statistical inferences that complement the results of conventional ERP methods (McIntosh & Mišić, 2013). Tarantino et al.

(2010) recently used PLSC to examine changes in the ERP that could account for the discrimination of brief durations.

PLSC decomposes and rotates brain data (e.g., ERP/fMRI/PET) using Singular Value Decomposition (SVD) to reveal latent variables (LV) that account for as much of the covariance between the brain data and the experimental design (e.g., contrasts and covariates) as possible. Each LV is then verified for statistical significance with a permutation test. The stability of an effect at a given time point is then obtained by bootstrapping, which gauges the variation of the LV by resampling. The smaller the variability, the larger the bootstrap ratio (salience at a given time point divided by its variability, akin to a z-score, Krishnan et al., 2011), the more stable an effect. These stable effects are said to contribute most to the significant LV. By permutation and bootstrapping, researchers can thus make inferences (e.g., difference in amplitude, correlation with covariates) based on the spatiotemporal characteristics of a LV. The measurement of interest is not limited to scalp potential per sampling time. For instance, Alin, Kurt, McIntosh, Öniz, and Özgören (2009) reported PLSC analysis using mean spectral power as the dependent variable.

Activities that are sensitive to experimental manipulations and covariates can be summarized by the electrode salience and the brain scores. The former summarizes the strength (value and sign of the salience) and stability (bootstrap ratio) in a spatiotemporal format. The latter summarizes how strong the salience is presented in each experimental condition. If the salience is positive, the relationships depicted by the brain scores can be directly interpreted as the differences between conditions; if the salience is negative, the brain scores have to be interpreted by first reversing the signs. Conditions show the largest difference if they attain brain scores of opposite sign (i.e., like a statistical contrast).

The number of latent variables is defined by the degrees of freedom after multiplying the number of levels from all factors. In the simplest case, when only two conditions are included in the PLSC, the analysis can be considered as a multivariate version of the difference wave analysis. PLSC was performed using the ERP module in the PLS toolbox in MATLAB (http://www.rotman-baycrest.on.ca/index.php?section=84). The number of iterations used for the permutation test was 500, and for the bootstrapping it was 1000, to ensure that inferences were made based on asymptotic distributions (Krishnan et al., 2011). Stable saliences are those effects with bootstrap ratio > 2.57 (a z-score significant at $\alpha = .01$), although > 2.00 ($\alpha = .05$) can also be considered (Krishnan et al., 2011).

Results

Bisection Parameters

Figure 3.2 shows the psychometric function by fitting the PLM to grand average p('long')s. For the PSE, one-sample *t*-tests showed that the subject PSEs did not statistically differ from the GM of 1600 ms, $M = 1684$ ms, $t(11) = .86$, $p = .40$, suggesting bisection at the GM (Allan & Gibbon, 1991). The mean DL was 262 ms, and the mean WF was .15, within satisfactory performance (Treisman, 1963) and the range obtained in previous bisection studies (Kopec & Brody, 2010). These results show that participants could perform the bisection task according to instructions.

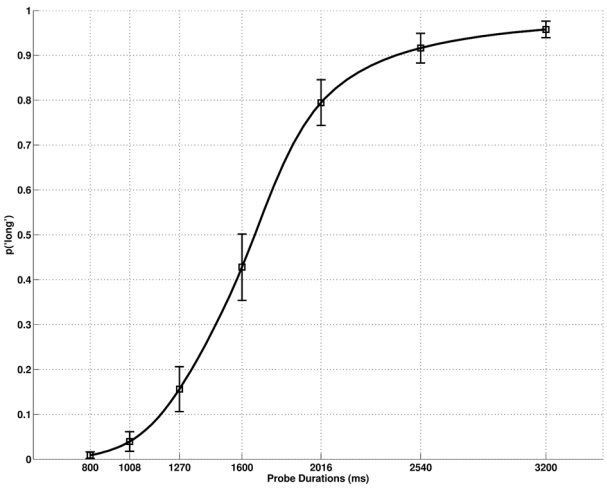


Figure 3.2. Grand average p('long') response function. Solid squares indicate mean p('long') at each probe duration. Error bars represent 95% bootstrapped CIs. The fitted curve is the PLM fit to the mean data.

Ex-Gaussian RTs

Figure 3.3 shows the mean ex-Gaussian *Mu*-s. One-way repeated measures ANOVA yielded a significant effect of Probe Duration, $F(6,66) = 12.56$, $p < .001$, ges = .30. Comparing each probe duration with the probe at GM (1600 ms) showed that *Mu* was similar until after the GM was exceeded (Table 3.1). This suggests that the central tendency of the intermediate probes that are close to the PSE/GM was not exceptionally slower than shorter probes. Once the GM had been exceeded, participants responded much faster.

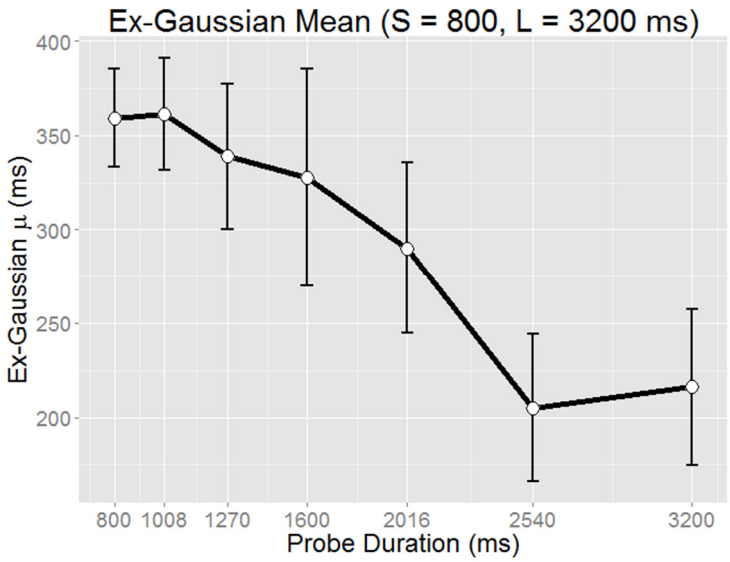


Figure 3.3. Mean ex-Gaussian *Mu* of each probe duration fitted on RT distributions approximated by a Gaussian kernel. Error bars represent within-subject 95% CIs.

Table 3.1

Summary of Contrasts on Ex-Gaussian Mu, with 1600 ms (Probe 4) as baseline

	Coefficient	*t*	p val
Probe 4 vs. Probe 1	31.53	1.031	.33
Probe 4 vs. Probe 2	33.73	1.042	.32
Probe 4 vs. Probe 3	11.31	.35	.73
Probe 4 vs. Probe 5	-37.41	-1.70	.12
Probe 4 vs. Probe 6	-122.64	-3.41	.0058**
Probe 4 vs. Probe 7	-111.49	-3.0080	.012*

Note: * indicates statistical significance at α = .05. ** indicates statistical significance at α = .0083.

Figure 3.4 shows the mean ex-Gaussian *Sigma*-s. One-way repeated measures ANOVA yielded a significant effect of Probe Duration, $F(6,66) = 5.82$, $p = .0091$, ges = .24. Using the same contrasts as *Mu* showed the same pattern, with the RT variability in most trials similar between the GM Probe and probes shorter than GM, but variability suddenly dropped after the GM had been exceeded (Table 3.2).

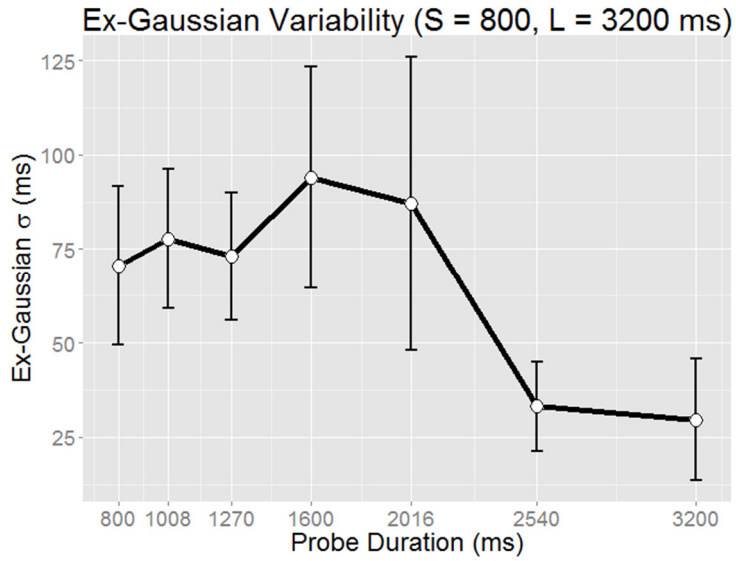


Figure 3.4. Mean ex-Gaussian *Sigma* of each probe duration fitted on RT distributions approximated by a Gaussian kernel. Error bars represent within-subject 95% CIs.

Table 3.2

Summary of Contrasts on Ex-Gaussian Sigma, with 1600 ms (Probe 4) as baseline

	Coefficient	*t*	p val
vs. Probe 1	-23.45	-1.22	.25
vs. Probe 2	-16.38	-.86	.41
vs. Probe 3	-20.92	-1.18	.26
vs. Probe 5	-7.016	-.49	.63
vs. Probe 6	-60.89	-3.97	.0022**
vs. Probe 7	-64.35	-3.94	.0023**

Note: * indicates statistical significance at α = .05. ** indicates statistical significance at α = .0083.

Figure 3.5 shows the mean ex-Gaussian *Tau*-s. One-way repeated measures ANOVA yielded a significant effect of Probe Duration, $F(6,66) = 7.044$, $p = .0047$, ges = .22. The same contrasts showed that there were more extreme RTs at the Probe = GM than the two shortest probes and the longest probe (Table 3.3).

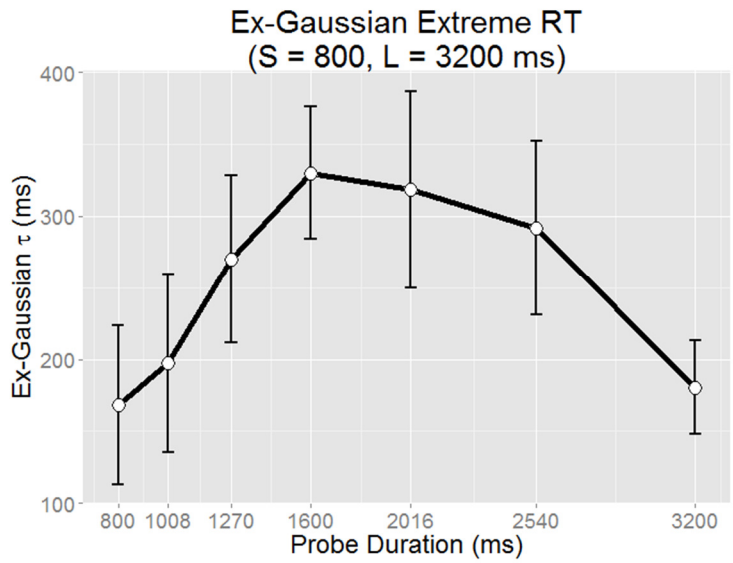


Figure 3.5. Mean ex-Gaussian *Tau* of each probe duration fitted on RT distributions approximated by a Gaussian kernel. Error bars represent within-subject 95% CIs.

Table 3.3

Summary of Contrasts on Ex-Gaussian Tau, with 1600 ms (Probe 4) as baseline

	Coefficient	*t*	p val
vs. Probe 1	-161.76	-4.63	.00073**
vs. Probe 2	-132.69	-3.33	.0067**
vs. Probe 3	-59.89	-1.61	.14
vs. Probe 5	-11.53	-.32	.75
vs. Probe 6	-38.040	-1.50	.16
vs. Probe 7	-149.35	-7.75	< .0001**

Note: ** indicates statistical significance at α = .0083.

EEG Component Verification

The first EEG analysis was done to confirm the presence of the CNV (Koenig & Melie-García, 2010). Grand average ERPs for each probe duration are shown in Figure 3.6. Presence of the CNV was confirmed by subjecting the participants' mean negative amplitudes at six FC/C electrodes to a one-sample *t*-test against zero. GFP showed that the CNV began at 246 ms after the P200 component. The mean amplitude in a time window common to all probe durations (246 – 800 ms) was -2.75 μV, which was significantly different from zero, $t(11) = -4.70$, $p = .0006$, 95% CI = [-4.04, -1.46] μV, confirming the presence of a negative ERP component. The spatial topographic map of the CSD in the same time window (Figure 3.7) shows a bilateral distribution over fronto-central electrodes, consistent with the S1-S2 CNV reported in previous studies (Macar et al., 1999; Pfeuty et al., 2003a, 2003b, 2005).

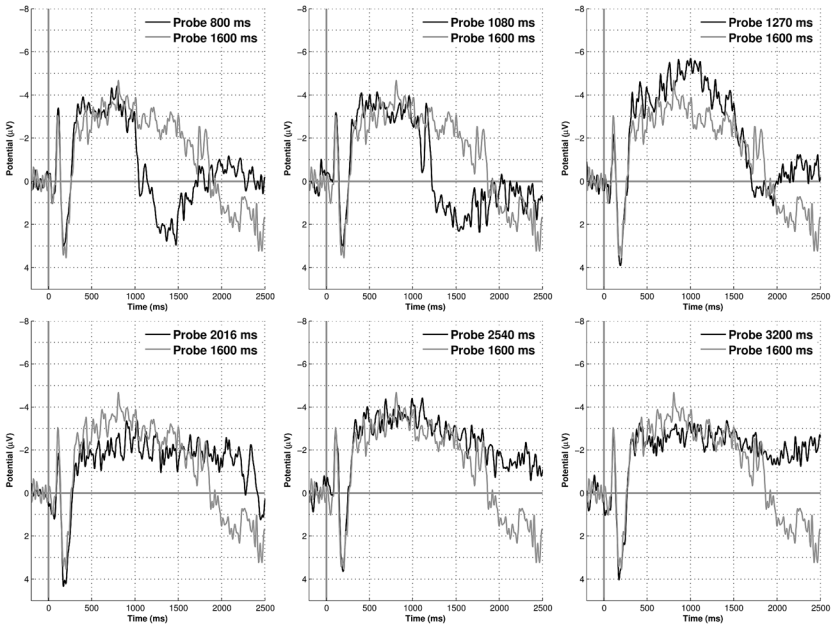


Figure 3.6. Grand average ERPs of each probe duration, collapsed across six fronto-central electrodes, smoothed with 8-point Gaussian sliding windows. The response to the 1600 ms probe duration (GM) is plotted in grey in each panel.

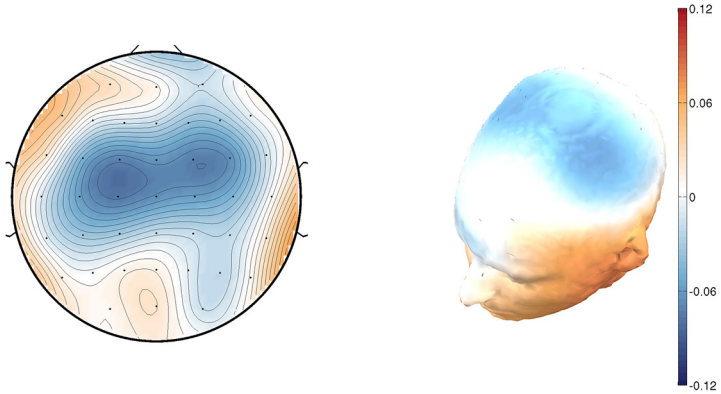


Figure 3.7. Topographical distribution of the CSD between 246 and 800 ms projected on a 2D and 3D head model. Unit is μV/cm^2.

Early Time Course of the CNV

These analyses addressed the question whether the CNV ramp is related to subjective time. ERPs were generated from all epochs because participants should not be able to discriminate among probe durations until at least 800 ms had passed. Global field power indicated a continuous increase in power after 246 ms, therefore we took the slope of the CNV amplitude between 246-800ms using least squares linear regression. Therefore, the unit of these slopes is μV/ms. Each set of 12 CNV slopes was tested against zero slope with a one-sample t-test. At 246-800 ms, M = -.0042 μV/ms and was significantly different from zero, $t(11)$= -3.59, p = .0042, 95%

CI [-.0057 to -.0014] μV/ms. It was also positively correlated with the participants' PSE, Pearson's $r = .67$, $t(10) = 2.76$, $p = .02$. However, mean CNV amplitude at the same time window was not correlated with mean PSE, $r = .42$, $t(10) = 1.41$, $p = .19$.

To examine the CNV right after S, we computed the slope 800-1354 ms (the same size as the previous time window) from probe = [1600, 2160, 2540, 3200 ms]. This slope was positive and statistically different from zero, M = .0014 μV/ms, $t(11) = 2.25$, $p = .046$, 95% CI [.00003 .0029] μV/ms. The change from the negative to the positive slope was significant, $t(11) = -5.96$, $p < .001$. Therefore, the CNV seemed to show an early peak at S.

Late Time Course of the CNV

Analyses of the late CNV time course addressed the question of whether changes in the CNV corresponded to the bisection criterion, which was close to the GM. To obtain a complete time course from stimulus onset to the GM, we generated the ERPs for each participant using trials at the two longest probe durations (i.e., 2540 and 3200 ms) that received a Long response. Longest probes were chosen because the shorter probes either terminated before or were too close to the GM. Only trials receiving a Long response were chosen because this indicated that the bisection criterion had passed in these trials. CNV slopes were obtained at three time windows near the GM: 1200–1600 ms, 1600 ms –AM (2000 ms), and AM-2400 ms. Table 3.4 shows the mean slopes and results of one-sample *t*-tests against zero. Only the positive slope between the GM and the AM was significantly different from zero, indicating a decline in CNV amplitude after the GM (Figure 3.8). However, the three slopes did not differ from each other, as indicated by a One-way repeated measures ANOVA $F(2,22) = .97$, $p = .35$.

Table 3.4

Summary of Mean CNV Slopes in 400 ms Time Windows

Time window (ms)	Slope (μV/ms)	One-sample *t*	p val
1200-1600	.0007	.65	.53
1600-2000	.0024	2.27	.0045*
2000-2400	-.0008	-.63	.54

Note: * indicates statistical significance at α = .05.

The change in CNV time course was also analyzed using mean amplitude. Six 200 ms time windows centered on the first six probe durations were constructed. The mean amplitudes of each time window were subject to a One-way repeated measures ANOVA with Probe Duration as the factor. This yielded a significant main effect, $F(5, 55) = 6.61$, $p < .001$, ges = .11 (Figure 3.9). To compare the changes among time windows, the mean amplitude at the 1600 ms probe was used as the baseline for comparison with every other probe duration mean amplitude (Table 3.5). Results showed that the amplitudes for the time windows preceding the GM were not significantly different from one another, while there was a marginally significant decrease in negative amplitude between the 1600 ms probe amplitude (GM) and the 2016 ms probe (16 ms after AM) amplitude, corroborating the slope analysis result.

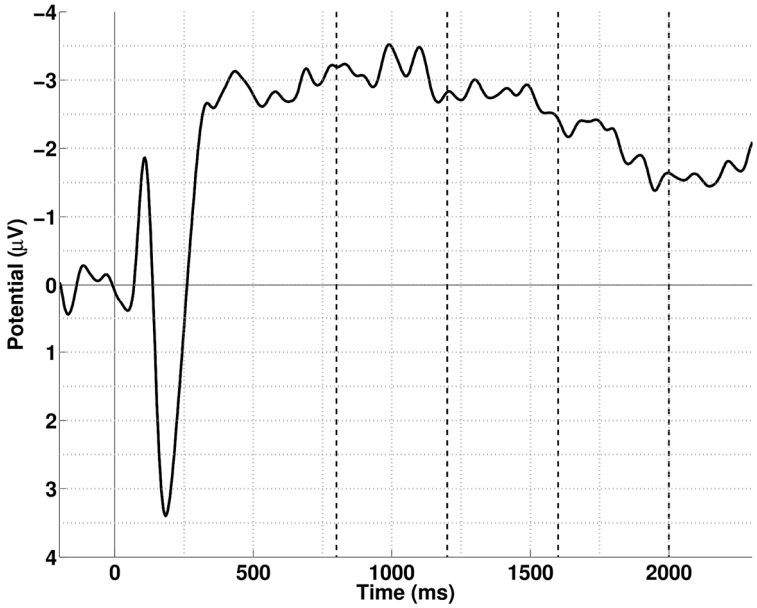


Figure 3.8. Grand average ERP of the two longest probe durations, averaged across six fronto-central electrodes. Thick vertical dotted lines demarcate the 400 ms time windows for which late CNV slopes were computed.

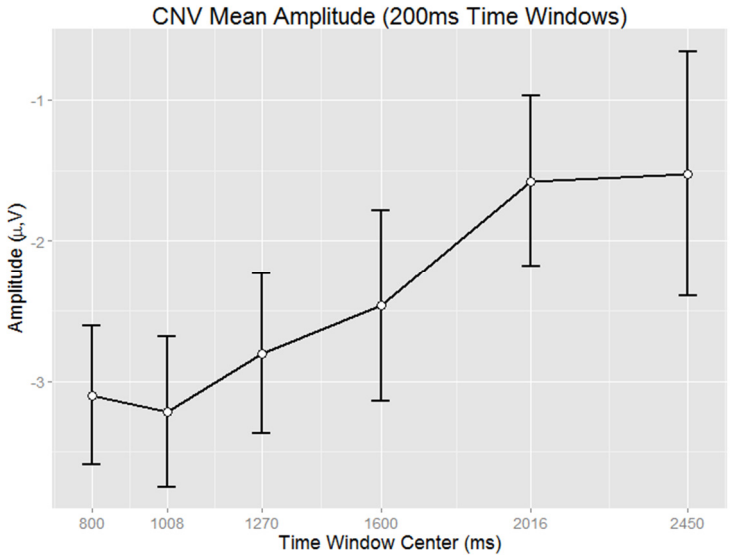


Figure 3.9. Mean CNV amplitudes at each 200 ms time window, centered at each probe duration. Errorbars represent within-subject 95% CIs.

Table 3.5

Summary of Mean CNV Amplitudes at 200 ms Time Windows compared against the GM Probe

	CNV Mean Amplitude (200ms)		
	coef	t	p val
vs. 800	-.64	-1.68	.12
vs. 1008	-.75	-1.97	.074
vs. 1270	-.34	-1.057	.31
vs. 2016	.88	2.15	.054
vs. 2540	.94	1.64	.123

The CNV Amplitude and Subjective Time

The next analysis addressed the question of whether there was a relationship between the CNV amplitude and subjective duration, by comparing ERPs generated from trials categorized as Short (RS) to those from trials classified as Long (RL), despite physically identical trial duration. Based on the *Tau* result as well as the location of the PSE, participants gave more comparable proportions of the two responses to the 1270, 1600, and 2016 ms probes. Therefore, subject average ERPs for each response type were generated using epochs from these intermediate probes, time-locked to the stimulus onset. These data were subjected to PLSC analysis (df = 1). The LV was not statistically significant, $p = 21$. Figure 3.10 shows the electrode

salience. The bootstrap ratio used was relatively modest (2.00, corresponding to z-score at $p = .05$), but no sustained stability was seen. Even at time samples with stable salience, the salience was negative, indicating that the ERPs of RS were more negative than RL, opposite to the pacemaker-accumulator hypothesis predictions. We also supplemented the multivariate PLSC analysis with a 'conventional' univariate permutation paired-sample *t*-test, examining the mean CNV amplitude between 246 and 1270 ms. It did not yield a significant difference between RS and RL at the fronto-central electrodes sites, $t(11) = -.77$, $p = .45$.

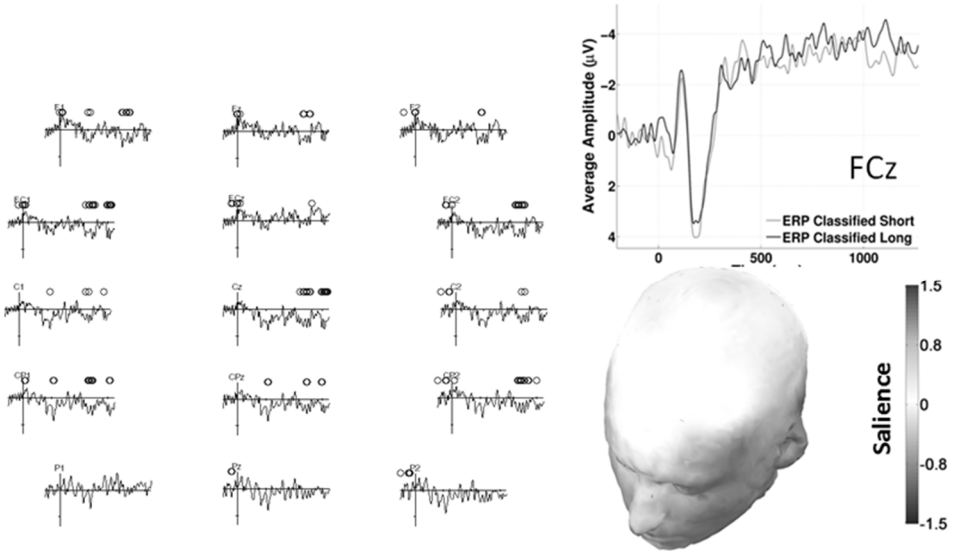


Figure 3.10. Left: Selected electrode salience of LV1 from the comparison between ERPs of RS and RL at the central electrodes. Time samples with stable salience are marked with circles at bootstrap ratio (absolute value) > 2.00. X-axis is time from -200 to 1270 ms. Y-axis is salience from -2.7 to 1.3, positivity plotted upward. Negative salience indicates RS being more negative than RL. Top Right: Grand average ERPs of each response at FCz. Bottom right: Topographical distribution of the voltage difference between the ERPs at the time window 246 -1270 ms. The white patch at the fronto-central sites indicates that the ERP difference was close to zero.

Positive Component at Duration Offset

Finally, we also examined what happened after the offset of the probe durations in light of a recent report from Lindbergh and Kieffaber (2013). They asked participants to perform a duration bisection task with S = 1250 and L = 3000 ms and their analysis focused on ERPs time-locked to the probe offsets. Using epochs from

all probe durations, they reported a larger positivity between 200 and 700 ms at the central electrode sites in the ERP associated with the Short response as compared to the Long response. They posited that the positivity reflected the memory comparison processes that were still ongoing for short probes, but already completed for long probes at the time of probe offset. These results suggest the functional relevance of post-offset positivity for time perception.

We averaged all the epochs time-locked to the probe offset. The baseline of the epochs was set to be the 200 ms pre-stimulus offset. The data was then subjected to a PLSC analysis (df = 1). The time window of interest was -200 to 700 ms relative to probe offsets. LV1 was statistically significant, $p < .001$. Stable salience (bootstrap ratio >= 2.57) was observed at parietal (positive) and frontal electrodes (negative) between 281 to 656 ms. This P300-like potential was preceded by a P2-like salience at 133-164 ms (Figure 3.11). Both components were more positive in the ERP from trials classified as short than those classified as long.

Performing the same analysis on the ERPs corresponding to trials classified as short or long (probe duration = 1270, 1600, and 2016 ms) yielded similar results (LV1 $p < .001$, not shown), which was not surprising because these data are just a subset of those in the current section.

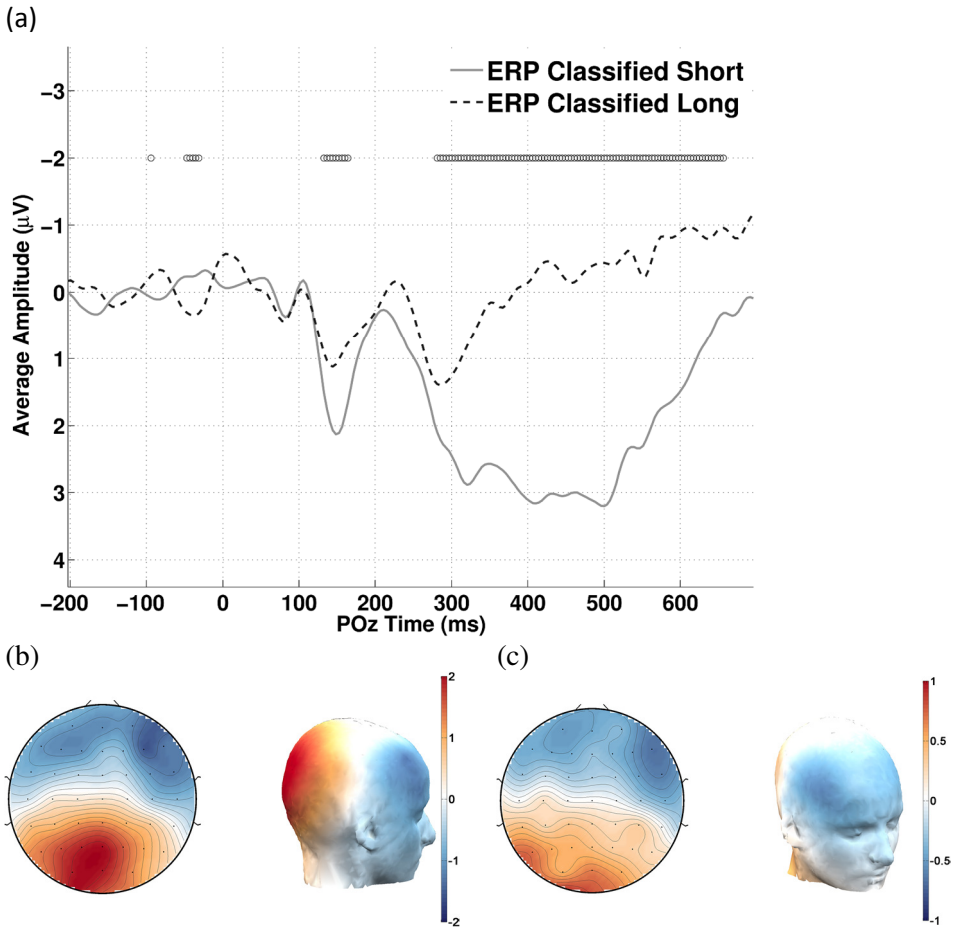
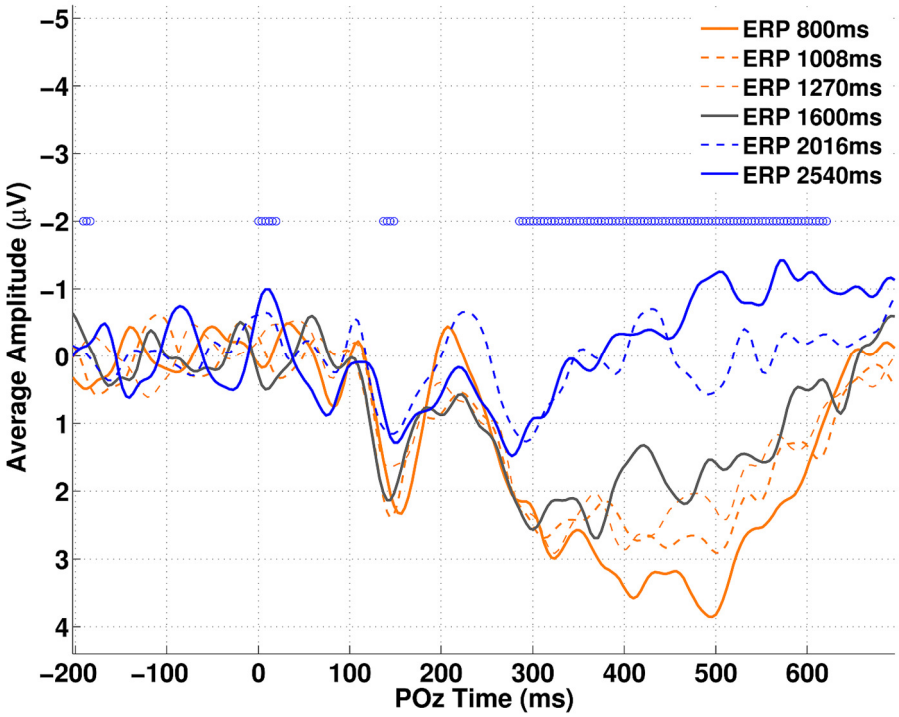


Figure 3.11. (a) The ERP from all trials classified as Short (Solid grey) as compared to the ERP from those classified as Long (Dotted dark grey) at POz. Stable difference (bootstrap ratio > 2.57) is indicated by the empty circles at the top of the panel. (b) The topographical distribution of the salience capturing the difference between the two ERPs at 281-656 ms. (c) The topographical distribution of the salience capturing the difference between the two ERPs at 133-164 ms. Positive difference indicates more positive amplitude in the ERP of Short responses.

Finally, to see if this positive component was sensitive to the probe durations and/or the criterion times such as S, L, and the GM, a similar PLSC analysis (df = 5) was performed on the positive component derived from each probe duration separately (cf. Kononowicz & van Rijn, 2014; Gibbons & Rammsayer, 2005). The preprocessing data epochs were too short for the 3200 ms probe durations so they could not be offset-locked and were not included in the analysis. However, the data pattern was quite clear and this exclusion is unlikely to have compromised the interpretation. Only LV1 was statistically significant, $p < .001$. It accounted for 69.44% of covariance. Similar to previous analyses, a P200-like salience at 137-148

ms and P300-like salience at 285-621 ms were observed (Figure 3.12). Specifically, the brain scores show that there was a gradual decrease in the ERP amplitudes as a function of probe duration; the brain score contrast was the greatest between probes shorter or equal to GM (positive brain scores) and those longer than GM (negative brain scores), a pattern that is also evident in the ERP plots (orange vs. blue). This 'boundary' is consistent with the idea that a bisection criterion expired after the GM.

(a)



(b) (c)

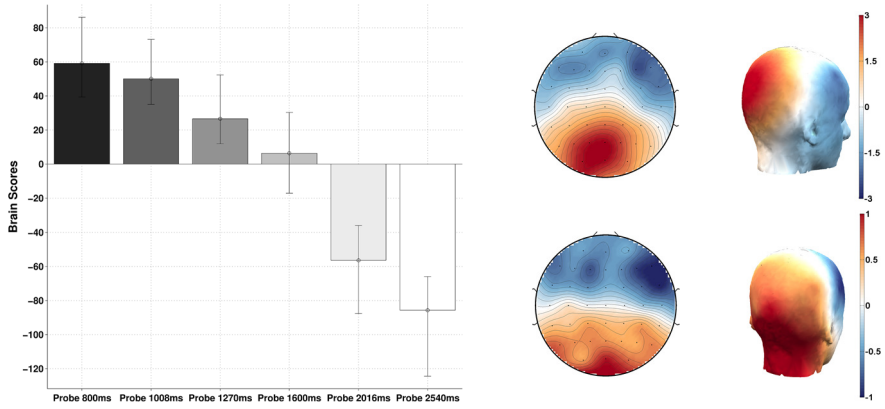


Figure 3.12 (Last page). (a) The ERPs from each probe duration at POz. ERPs from probes shorter than GM (1600 ms, black) are in orange, while those from probes longer than GM are in blue. Stable difference (bootstrap ratio > 2.57) is indicated by the empty circles at the top of the panel. (b) The brain scores corresponding to LV1. Brain scores best separated the ERPs corresponding to probe durations shorter than GM from the longer ones. (c) Top: the topographical distribution of the salience capturing the differences among the ERPs at 285-621 ms. Bottom: the topographical distribution of the salience capturing the differences among the ERPs at 137-148 ms. A positive difference indicates more positive amplitude in the ERPs of shorter probes.

Discussion

Multiple sources of temporal information are present even in the simplest timing tasks. Humans and non-human animals are very apt at extracting the necessary information and flexibly adapting when it changes (Balci et al., 2011). Interval timing performance in humans and non-human animals has been successfully explained by the Scalar Timing Theory (STT; Church et al., 1984). The pacemaker-accumulator model is an information processing conceptualization of this theory and is argued to be instantiated in the brain (Macar et al., 1999; Simen et al., 2013). The CNV is regarded as the EEG evidence for this model (Casini & Vidal, 2011). In this experiment, we examined whether changes in the CNV in the duration bisection task are consistent with this model.

Our results show that participants had more extreme RTs at probe durations near to the GM, implying more difficulty in making a decision at these probes (Gu & Meck, 2011). These behavioral data were corroborated with ERP data. The CNV indicated a decision criterion in the middle of the long probe durations, so that participants did not wait for the whole duration to elapse to engage in post-trial decision making. Moreover, the positive component after probe offsets was larger for trials classified as Short than Long, suggesting differences in the decision process (Lindbergh & Kieffaber, 2013; Paul et al., 2011).

More specific to the pacemaker-accumulator model predictions, the CNV resolution coincided with the bisection criterion at the PSE/GM, and the CNV ramp rate was correlated with the PSE; however, the average CNV amplitude from trials receiving a long response was not more negative than that from trials receiving a short response.

The Bisection Criterion

Psychometric results. Using a geometric series between 800 and 3200 ms, we obtained subject PSEs that were close to the geometric mean (GM), consistent with animal and human studies (Stubbs, 1976; Allan & Gibbon, 1991). The subject WFs were within the range reported in previous studies, indicating that participants performed the task at a satisfactory level. In the meta analysis by Kopec and Brody (2010), the WF for an S:L ratio of 1:4 ranged from .1 to .35.

Response Time. The *Mu* and *Sigma* components did not show statistically significant differences among probe durations that were shorter or equal to the GM, but both were significantly smaller for the two longest probe durations. In contrast, *Tau* showed that there were more extreme RTs at probe durations near the GM than those more differentiable from it. This suggests that participants were slower in some trials of the probe durations near the PSE/GM, but not in other trials.

These results are consistent with the findings reported in Droit-Volet and Izaute (2009). In one of the experiments, they allowed adults and children to answer 'I don't know' instead of a forced choice in the bisection task. In adult participants, the number of 'I don't know' response was the most at the probe duration closest to the AM. However, they did not do so in all trials, and managed to assign a choice on the remainder of the trials. According to Scalar Timing Theory, temporal memory has a Gaussian distribution. Therefore, the sampled bisection criterion may be shorter in some trials and longer in others, allowing the difference between the criterion and the current time to be bigger than the decision threshold. Participants would not encounter any difficulties in responding to these supra-threshold trials. Furthermore, the authors speculated that when the adult participants responded 'I don't know', they perceived the probe duration to be neither short nor long. Hence, for the present data the lack of a difference in the *Mu* and *Sigma* components for trials close to the GM may be due to a subset of trials in which participants had no problem assigning a

choice, whereas *Tau* reflects the subset of trials in which the probe duration was ambiguous. Hong and Beck (2010) showed that the entropy in the RT of a visual target detection task increased (more wide-spread RT distribution) with increased uncertainty in spatial (more possible target locations) and temporal information (more possible inter-target intervals). Thus, uncertainty in the decision produces the longer tail in the RT distribution.

The RTs of probe durations longer than the GM gave the smallest estimates for all three parameters. This further supports the location of the bisection criterion to be at the central tendency of the probe series. The participants had enough information to make a decision as soon as the GM or PSE was reached, but because they had to wait for the end of the signal to respond, the remainder of the trial became a simple reaction time task with a foreperiod (Kristofferson, 1977; Niemi & Näätänen, 1981). Moreover, the bisection criterion became an S1 cue for temporal orientation for the offset of the duration (S2; Miniussi et al., 1999).

The CNV and the Pacemaker-Accumulator Model

Peak and resolution. The negativity elicited shared the same EEG and CSD topographies as the CNV in S1-S2 anticipatory and duration estimation tasks (Gibbons & Rammsayer, 2004; Pfeuty et al., 2005; Praamstra et al., 2006). Analyses of the changes in the CNV slope across time of probe durations longer than the GM (2540 & 3200ms, receiving a Long response) showed that the negative potential did not ramp up all the way until the end of the probe, as would be expected from an accumulation process, but instead peaked at S. If the peak latency reflects the temporal decision criterion (Macar & Vidal, 2003; Mento et al., 2013), this would imply that S comprises one piece of critical temporal information in the bisection task. The sensitivity to S is consistent with some of the proposed temporal decision making mechanisms. For instance, in the model proposed by Kopec and Brody (2010), participants first decide whether the probe duration is S, L, or neither. If it is neither,

they compare the ratio of the distance between S and the probe to the distance between L and the probe. Penney et al. (2008) observed a systematic categorical reversal in the response functions in humans, rats, and pigeons when the task was difficult (e.g., very small S:L ratio of 1:2). They also proposed a two-step decision model, in which the first step requires the test duration to be discriminated against a boundary time M, and the second step requires the differences between the probe duration and each anchor to be evaluated. If these models are implemented in the neural networks, the memory of S (and L) is needed. The CNV at S might reflect this kind of decision rule in action.

As discussed in Chapter 2, decision models involving only S and L cannot account for the effect of the distribution of the probe durations on the PSE location. In fact, after reaching the early peak at about S the CNV was sustained until the GM and then began to return to baseline. As shown in the behavioral analyses, this duration was likely the bisection criterion. Therefore, the assertion that the CNV amplitude resolution indicates the end of temporal pulse accumulation is supported. Once the bisection criterion was reached, there was enough temporal information for a certain binary decision. There was no need for further accumulation (Macar & Vidal, 2003).

That the PSE is at GM rather than arithmetic mean (AM, 2000 ms) is consistent with prior work in both human (Allan & Gibbon, 1991) and non-human animals (Stubbs, 1976). However, it is premature to conclude that animals represent mental constructs such as time in a logarithmic scale, because a few studies have shown that linear representation of time can create behaviors that follow the logarithmic rule (Gibbon, 1981; Simen et al., 2013). While it is more likely to observe the bisection at GM when the probe distribution is logarithmic (Allan & Gibbon, 1991), the meta-analysis by Kopec and Brody (2010) concluded that the PSE is in general below the AM regardless of the probe distribution.

These changes in the CNV time course imply that for durations longer than the GM, the CNV did not increase till the end of the probe. Logically, participants would need to be sensitive to the long anchor, because the range of possible durations contributes to timing performance (Brown et al., 2005; Jazayeri & Shadlen, 2010; Klapproth & Müller, 2008). For instance, Klapproth (2007) asked participants to reproduce visual stimulus durations of 15, 30, and 45 seconds under prospective and retrospective timing conditions. In retrospective timing, participants are not told that they have to time the event until they have finished it. Timing performance is usually vastly different between prospective and retrospective timing (Zakay & Block, 2004), but they were made comparable in this study by asking the participants to respond to the visual stimulus immediately after it terminated. This raised participants' awareness of time so that they timed the stimulus despite the absence of a timing instruction. The same temporal relevance of the stimulus may have occurred after the criterion time was reached during the longer probe durations because the participants still needed to respond at the duration offset, which led them to time the remainder of the stimulus. In addition, ERPs corresponding to attended and unattended timing are sensitive to the difference between the standard/criterion time and the test/probe duration, regardless of whether the latter is shorter or longer than the former (Kononowicz & van Rijn, 2014; Tse & Penney, 2006). This sensitivity is only possible if timing continues after the criterion time has elapsed. Finally, other studies showed that the CNV amplitude was not modulated by the duration being timed at all (Elbert et al., 1991; Gibbons & Rammsayer, 2004). In this regard, the extent to which the CNV reflects critical durations may depend on the task and the availability of different timing information in the context, making the interpretation of the CNV as the biomarker of an accumulator conditional on the task. Since it is unlikely that timing tasks relying on single duration comparison should differ in their underlying duration estimation mechanisms (Merchant, Zarco, Bartolo, & Prado, 2008) unless

otherwise proven, the current version of the pacemaker-accumulator model and its predicted changes in the CNV awaits a systematic account for when the CNV best reflects an accumulator process.

Amplitude. Consistent with the accumulator hypothesis, analyses of the initial ramping after the auditory N1P2 complex (240 ms – S) showed that the slope, but not the amplitude, was positively correlated to the PSE. It is proposed that (e.g., Durstewitz, 2004; Pfeuty et al., 2003b, 2005) the slope of the CNV reflects the rate of temporal accumulation. Hence, a shallower CNV slope means slower temporal accumulation, which results in a smaller perceived (i.e., subjective) duration for a given objective duration. However, given the proximity in the time of presentation of the anchors and the probes, a slower accumulator should also apply to the anchor durations, maintaining the relative differences among the anchors and the probe durations. A possible solution is that the slow accumulation occurred on some trials only, and these probe durations were compared to a relatively stable representation of the bisection criterion or the anchors. Treisman (1963) proposed a clock mechanism that emits pulses at different rates across trials and used this variability to explain the scalar property instead of attributing the variance to the memory and decision stages (Gibbon, 1977). Such mechanisms allow the clock to be slower in some trials than the others.

However, differences in the CNV amplitude could not differentiate between ERPs from trials classified as Short and those from trials classified as Long, adding to the equivocal evidence of the link between CNV amplitude and subjective time. Neither the multivariate or univariate approach yielded any discernible differences in amplitude at the fronto-central electrode sites. This does not support the proposal that the CNV reflects temporal memory resulting from neural integration (Macar &Vidal, 2004).

What the CNV may Reflect

The changes in the CNV do not provide very strong evidence for its interpretation as a biomarker of a pacemaker-accumulator process. The presence of a CNV resolution at the bisection criterion, but absence of the amplitude changes associated with subjective duration (a change in response) could mean that the CNV reflects temporal decision making processes that are dissociable from the temporal memory or temporal evidence accumulation, so that it represents the end product of the clock mechanisms, but does not constitute direct evidence of what the clock mechanisms may be like. Admittedly, even the CNV resolution was not a particular strong effect, as the changes in the CNV slope across time windows were not significant. In fact, the CNV generated from long probe epochs in our experiment appears to be 'flatter' in time course as compared to previous S1-S2 studies using slightly shorter durations. As will be illustrated in subsequent chapters, this 'flat' CNV shape was quite consistent across experiments whenever longer durations were used. Specifically, the CNV obtained in S1-S2 studies appear to have a more well-defined ramp to the peak (Macar & Vidal, 2003; Pfeuty et al., 2008). Tecce (1972) classified two types of CNV in an early review. Type A has a sharp rise to peak and is believed to reflect temporal uncertainty of S2 occurrence, while Type B has a more gradual rise, but its morphology looks more like a ramp overall, reflecting higher temporal certainty. His Figure 3 also shows that the Type A CNV does not give as clear a peak as Type B. The CNV observed in Experiment 1 might be classified as a Type A CNV, because the relatively large absolute difference between the short (800 ms) and the long anchor (3200 ms) could suggest larger uncertainty about when the probe may terminate (Niemi & Näätänen, 1981). The difference in absolute duration between the current study and previous studies is not likely to be the only factor modulating the type of CNV manifested. For instance, in the explicit motor timing task of Praamstra et al. (2006), the inter-cue interval was 1500 to 2000 ms, but the CNV elicited had the distinct ramp and peak of a type B CNV, due to the high

certainty of the time of occurrence of the next cue. Mento et al. (2013) demonstrated a clear single-peak negative slow wave in an oddball task, in which the standard visual duration was 1500 ms. This echoes the earlier speculation that the manifestation of the CNV may be highly dependent on the task characteristics.

Furthermore, CNV amplitude was relative stable between S and the bisection criterion. It could be that the short anchor and the bisection criterion demarcated the critical time window during which sustained attention was required to keep track of time in order to emit a response. Decrease in attention is known to result in decreased subjective estimation of time (e.g., Brown, 1997). CNV is also modulated by attentional demands. For example, Campbell et al. (2009) asked participants to respond to a 20 ms gap that appeared early (300 ms) or late (1300 ms) in an otherwise continuous 1400 ms tone when the tone frequency was 500 Hz, but not when it was 1500 Hz. A sustained slow negative wave (SNW) related to sustained auditory stimulation was present in all conditions regardless of response requirements, but the ramping CNV was present, superimposed on the SNW, only when it was a low-tone trial. Similarly, Tecce (1979) and Travis and Tecce (1998) recorded participants' CNV when they performed a fixed foreperiod experiment. In the control block, participants responded to an auditory imperative stimulus as quickly as possible after a fixed supra-second foreperiod. In the experimental block, they had to perform a concurrent letter recall task during the foreperiod in some trials, but not the others. Among all three trial types, the letter task condition triggered the smallest CNV, while the no-letter task condition showed a rebound effect, triggering an even more negative CNV than the control condition. The authors argued that attention was distracted away in the letter task condition, resulting in a smaller CNV, while more attention was devoted in the no-letter task condition once the participants knew that it was a trial without distractor. By the same token, the CNV in the bisection task could be indexing the degree of attention paid, which is essential to the clock mechanisms,

but not the pacemaker-accumulator process *per se* (van Rijn et al., 2011). It rose until S and dropped at the PSE, but showed no amplitude modulation by subjective duration because it reflected the general level of sustained attention (Macar, Grondin, & Casini, 1994), which could be disengaged once enough evidence (between S and PSE) had been gathered for the temporal decision. Attention is just one of the several sources of duration variability, so it may or may not differ when there was a change in response.

The Offset Component

The larger positivity associated with the offset of probe trials that received a short response regardless of probe length was taken as evidence of the comparison process (Lindbergh & Kieffaber, 2013). As the psychometric functions showed, trials receiving a short response were predominately of durations shorter than GM. It is argued that in these trials, the participants were still engaging in the comparison process. Furthermore, it is possible that the more similar the probe duration and the GM, the stronger the response competition because short and long responses were equally likely, resulting in longer reaction time (Kristofferson, 1977; Wencil, Coslett, Aguirre, & Chatterjee, 2010). Processes like this might have contributed to the positive component that had a parieto-occipital distribution. On the other hand, Rockstroh et al. (1993) found that stimuli presented during the period of the CNV gave larger perceptual ERP components such as P2/P300. They proposed that since CNV reflects enhanced cortical excitability, the larger components are a result of this increased activation. Therefore, the larger positive component observed in trials receiving a short response may be a result of a positive component 'riding' on a still activated cortical network. This would imply that toward the end of these trials, participants were still engaged in timing or attending (CNV present) because they were expecting the internal bisection criterion (Coull et al., 2000), which was no longer the case after the criterion had passed (CNV resolved).

The topography and polarity of the later offset component suggests that it might be the P300, an ERP component triggered after stimulus evaluation (e.g., matching with memory and/or expectancies; Donchin & Coles, 1988; Verleger, 1988) and that is associated with decision-making (Nieuwenhuis, Aston-Jones, & Cohen, 2005). It is also argued that the occurrence of the P300 may be conditional on the occurrence of negative slow waves such as the CNV (e.g., Kok, 1978; Le Dantec et al., 2007), with the CNV providing the context for the functions reflected by P300 (Birbaumer & Elbert, 1988; Deecke & Lang, 1988). Specifically, this negative slow wave – positive slow wave sequence was found to be larger in timing than non-timing tasks, revealing stronger and wider activation of neural populations in the former. For instance, Gibbons, Brandler, and Rammsayer (2003) asked participants to perform temporal generalization and pitch discrimination on identical auditory stimuli. While behavioral performance indicated that participants were less accurate in discriminating pitch, the amplitudes of the slow waves were larger in the temporal generalization task. This pattern remained when participants were divided into better-timing/worse-pitch-discrimination and better-pitch-discrimination/worse-timing groups. The authors proposed that these results implicate a stronger involvement of working memory in timing, even when durations are as short as 200ms.

To further validate the function reflected by these positive components, Gibbons and Rammsayer (2005) compared timing to passive-listening to brief tones (ranging from 125 to 275ms). ERPs were timelocked to tone onset. Two positive potentials, a parietal P300 and a frontal P500, were elicited only when duration estimation was required. The P300 decreased in amplitude as duration increased, whereas the P500 was larger whenever the durations were non-targets. In contrast, they were not modulated by variation in tone pitch. The authors postulated a two-stage model for processing brief durations. First, the duration-modulated, parietal P300 was interpreted as the classic memory-based P3b timelocked to stimulus onset,

which indicates an immediate temporal processing of the stimulus. This component is not revealed for longer durations because of the presence of the CNV due to the expectation of stimulus offset (Loveless & Sanford, 1974. It is maximal for durations shorter than the target because evaluation of the whole stimulus duration can only be completed when the stimulus is short and the CNV does not occur when durations are too brief.

Second, the duration-insensitive, fronto-central P500 component was interpreted as a novelty P3a time-locked to the expected duration offset at the target duration (200ms) and thereby indicating a violation of expectation, a situation that would happen as long as the stimulus was a non-target (Kristofferson, 1977). Interestingly, the absolute difference between the target and the non-target did not influence the amplitude of this P3a. This is in contrast to the findings in mismatch negativity (Tse & Penney, 2006) and the evoked potentials of the duration offset marker (Kononowicz & van Rijn, 2014) that the amplitude of these components varied according to the difference. The offset positivity obtained here, which decreased in positivity when the probe durations were longer, did not fit uniquely to either component, although its topography and sensitivity to stimulus duration suggests that it resembles a memory-based P3b.

The positivity preceding the P3 like component resembles the P200 corresponding to tone offset in terms of its latency, although its topographical distribution does not agree closely. Early studies both pointed to overlapping and distinct neural correlates between an offset stimulus and the offset of a continuous stimulation (i.e., the stimulus is simply withdrawn; Noda et al., 1998; Pantev, Eulitz, Hampson, Ross, & Roberts, 1996). More importantly, this component was more positive when probes were shorter or equal to GM. This is partly consistent with Kononowicz and van Rijn's (2014) findings that the N1P2 amplitude of the offset marker in their temporal discrimination experiments (durations = 1, 2.2, and 2.5

seconds) decreased as the probe duration was closer to the target duration. However, this relationship broke down in our experiment when durations were longer than the GM, while it was preserved in their experiments (i.e., the N1P2 amplitude showed a V-shaped relationship with duration). Differences in experimental design might account for some of these discrepancies. Particularly, a response did not have to be made at the offset of the duration, but 3 or 5 seconds after the offset, when a response cue was presented. As argued above, participants might show larger temporal awareness in this case and engage in implicit timing, because they were not distracted by the motor task.

To conclude, examination of behavioral, CNV data, and the offset positive component during the duration bisection task suggests that participants were sensitive to the short anchor and the bisection criterion. Among our findings, the time course of the CNV (ramp stopped at S) and the relationship between CNV amplitude and subjective time (absence of amplitude difference between trials classified differently) were not consistent with a pacemaker-accumulator account of the CNV (Macar et al., 1999; Pfeuty et al., 2005), while the positive correlation between the CNV ramp slope and PSE as well as the CNV resolution at the GM were consistent with the proposition (cf. Macar & Vidal, 2004; Pfeuty et al., 2005), but not without further assumptions. Therefore, our results do not strongly support the pacemaker-accumulator or climbing neural firing hypothesis (van Rijn et al., 2011). The current and previous studies suggest that ERPs corresponding to stimulus offsets may be modulated by the difference between test duration and target duration, regardless of task. Further studies should focus on these components to determine their functional implications in duration estimation.

Chapter 4 Investigating the Bisection CNV Using Probe Durations from Different Anchor Durations

The behavioral and ERP results from Experiment 1 provided relatively weak support for a relationship between the CNV properties and a pacemaker-accumulator process. However, having only one duration range also prevented examination of the remaining prediction given by the pacemaker-accumulator hypothesis:

a) The shorter the target duration, the more rapid the ramp of the CNV (Pfeuty et al., 2005) and the earlier resolution of the CNV maximum negativity (Macar & Vidal, 2003). This neural activation pattern enables duration discrimination when

b) The CNV amplitude at the criterion time is constant (Pfeuty et al., 2005). The maximal amplitude of the CNV has been argued to be related to the decision criterion (Boehm, van Maanen, Forstmann, & van Rijn, 2012; Loveless & Sanford, 1974; Ruchkin et al., 1986). The modified pacemaker-accumulator model proposed by Simen et al. (2013) suggests that this criterion should always be set near the maximal neural activities, since the adjustment of this threshold is more difficult than other properties (e.g., tuning neural firing rate) in real neural systems.

On the other hand, the latency of the early CNV peak (about 800 ms) at S observed in Experiment 1 coincided with the peak latency typically reported for the O-wave, an orienting response to the stimulus onset (Rohrbaugh et al., 1978; Tecce, 1972). If the O-wave is sensitive to the short anchor, its latency should be a function of the anchor. This could not be shown with only one anchor pair in Experiment 1.

Therefore, we used more than one set of anchor and probe durations in Experiment 2, so that there were two different short anchors and bisection criteria. This can be done by using a different short anchor while keeping the long anchor unchanged. However, this also changes the S:L ratio, which may influence the difficulty of the bisection task (Penney et al., 2008; Wearden & Ferrara, 1996).

Changing the distribution of the probe durations (cf. Brown et al., 2005) may also lead to the same result. Therefore, we decided to change the absolute durations across the two sessions, so that participants performed two bisection tasks that were comparable in terms of temporal discriminability. Kopec and Brody's (2010) meta-analysis on the effect of absolute duration on the PSE also indicated that for a given S:L ratio, the ratio of the bisection criterion to the arithmetic mean of the anchor durations was not affected by the absolute duration of the anchors.

If the CNV does not reflect a pacemaker-accumulator process, we expect the CNV shape to change more 'liberally'. Specifically, we expected a Type B CNV when the anchor durations were short, and a Type A CNV when the anchor durations were long.

To summarize, we predicted that under the pacemaker-accumulator hypothesis, 1) the shorter the GM, the steeper the CNV ramp, 2) the shorter S, the earlier the CNV amplitude plateaued, 3) CNV amplitude at the bisection criteria would be constant regardless of absolute duration, and 4) the longer the GM, the later the CNV resolution, and the time of resolution should correspond to the PSE.

Method

Participants

Sixteen students (aged 19-44 years, eight female) from the National University of Singapore gave informed consent and took part in a two-session duration bisection experiment. Fifteen participants were right-handed according to the Edinburgh Handedness Inventory. They were naïve to the hypotheses of the experiment and were reimbursed for their participation at a rate of SGD10/hr.

Stimuli

The auditory tones were identical to those used in Experiment 1 except in their durations. Two sets of five logarithmically distributed probe durations, including

the anchors, were used. These were 1060, 1400, 1852, 2450, 3240 ms (Session Long) and 600, 800, 1060, 1400, 1852 ms (Session Short), respectively. A stimulus duration set size of five was previously used in the bisection task by Allan (2002b). The psychometric functions were highly similar to those in subsequent experiments using more probe durations. In the present experiment, the two sets overlapped so that there was a set of common probes (1060/1400/1852 ms).

Procedures

The duration bisection task was similar to that used in Experiment 1 with the following exceptions.

Participants took part in two bisection sessions separated by at least one week. The two sessions differed in the durations of anchor/probe used. In Session Long, auditory probes with longer absolute durations were used: S = 1060 ms, and L = 3240 ms. In Session Short, the anchor durations were shorter: S = 605 ms, and L = 1852 ms. The S:L ratio was the same for the two sessions (~1:3.06), and only slightly smaller than that of Experiment 1 (1:4). The PSE is typically close to the geometric mean of a probe duration series when the S:L ratio is between 1.8 and 4 (Kopec & Brody, 2010). The order of Session Long and Short was counterbalanced across participants.

Each session was divided into seven short blocks of eight minutes each. The last block differed from the first six in instructions and was originally designed for comparison with the preceding blocks; however, given its fixed order (always the last) and its relatively small number of trials, we do not discuss it further in this dissertation. Results from the first six blocks are reported. Each block began with the learning of the two anchors. Each anchor was presented five times in randomized order. During the test phase, each probe duration was repeated fifteen times (a total of 90 trials per probe). Presentation order was pseudo-randomized so that each probe was preceded by a nominally 'short' probe, 'long' probe, or the middle probe at the GM (1852 ms in Session Long and 1060 ms in Session Short) as equiprobable as

possible, using the Mix program (van Casteren & Davis, 2006). After hearing each probe, participants pressed one of the two response keys with their index fingers to indicate their choice. The time window for response was 3000 ms following probe duration offset.

Scalp EEG Recording Set Up

The EEG set up was similar to that of Experiment 1 with the following exceptions. Data were processed offline separately for each session with the same procedures. After the data was band-pass filtered (0.1-32 Hz) and visually inspected for artifacts and bad channels, the continuous data was average referenced and epoched prior to ICA. The epoch started from 1200 ms prior to stimulus onset to 4000 ms after stimulus onset. Average reference was used for better visualization of slow drifts in bad channels. Debener, Thorne, Schneider, and Viola (2010) commented that this change does not usually alter the preprocessing results. This was verified by preprocessing the data from this experiment both ways, which resulted in highly comparable outcomes. Due to technical errors, three blocks of EEG data from three different participants were not recorded (3 out of 6 x 2 x 16 = 204 blocks = 1.56%).

Results

Bisection Parameters

Estimates of PSE, DL, and WF were computed for each session and participant. Figure 4.1 shows the grand average psychometric functions. For PSE, one-sample *t*-tests showed that the subject PSEs from Session Long were marginally shorter than the geometric mean (GM) of the probe duration series ($p = .055$), while the subject PSEs from Session Short were at the GM (Table 4.1). Their 95% confidence intervals (CI) did not overlap, indicating a statistically significant difference between the PSEs of the two sessions. For DL, a paired-sample *t*-test showed that the temporal sensitivity in Session Long was lower than Session Short, $t(15) = 5.75$, $p < .001$. For WF, the sessions did not differ, $t(15) = .20$, suggesting that

the temporal sensitivity difference was the same after mean estimation adjustment, so the difficulty of the two bisection sessions was comparable. This is further illustrated by the superimposition of the two functions (Figure 4.2).

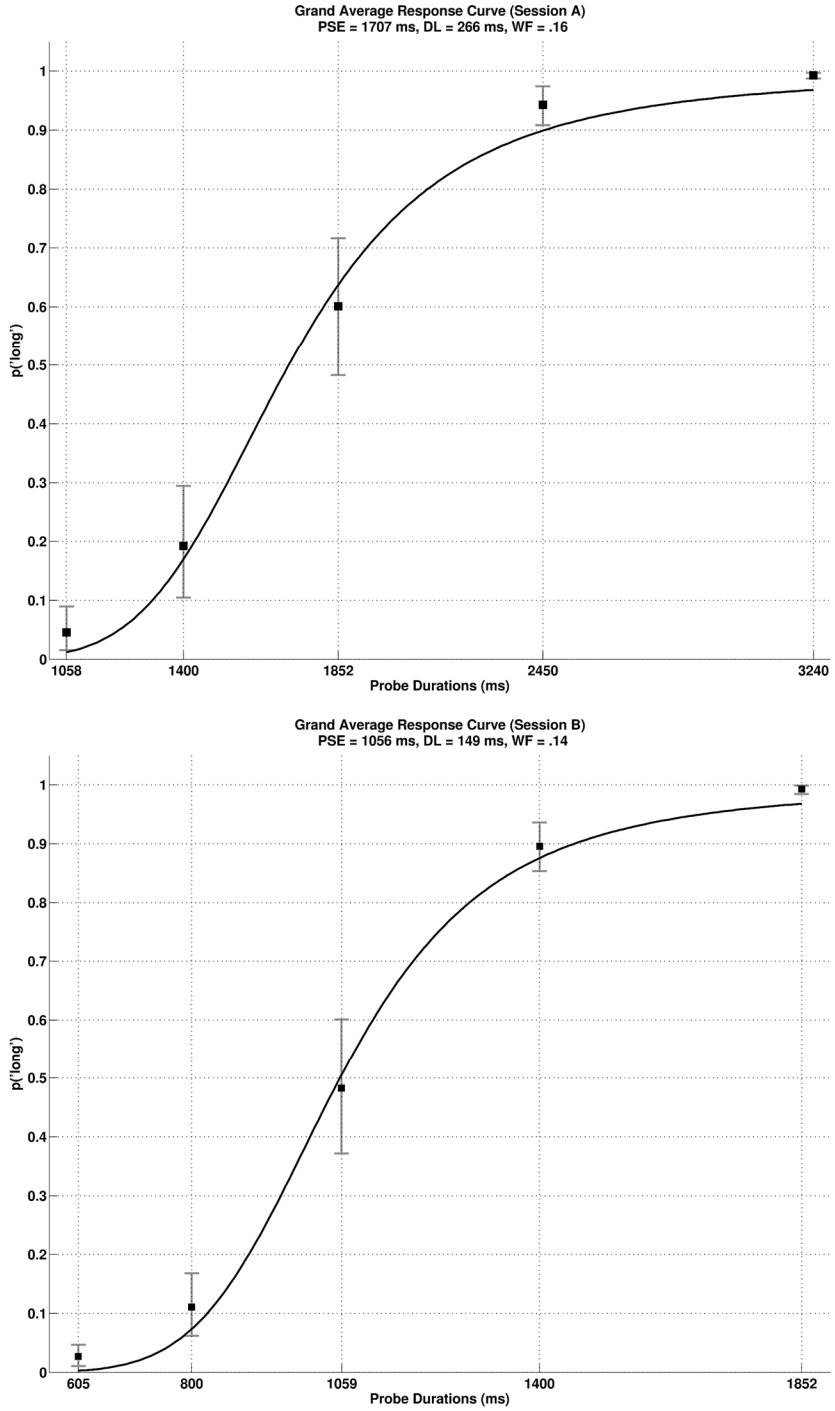


Figure 4.1. PLM fit (black smooth curves) of Session Long, which used longer S and L (top) and of Session Short, which used shorter S and L (bottom). Group average p('long') response data are indicated by filled squares, with error bars representing 95% bootstrapped confidence intervals (CIs).

Table 4.1

Summary of Mean PSEs and One-sample t-tests Against the Geometric Mean (GM)

Mean PSEs against GMs				
Condition	PSE (ms)	GM (ms)	*t*	p val
Long	1717 (+/- 74.66)	1852	-2.08	.055
Short	1058 (+/- 74.12)	1060	-.074	.94

Note: Values in brackets indicate 95% CIs.

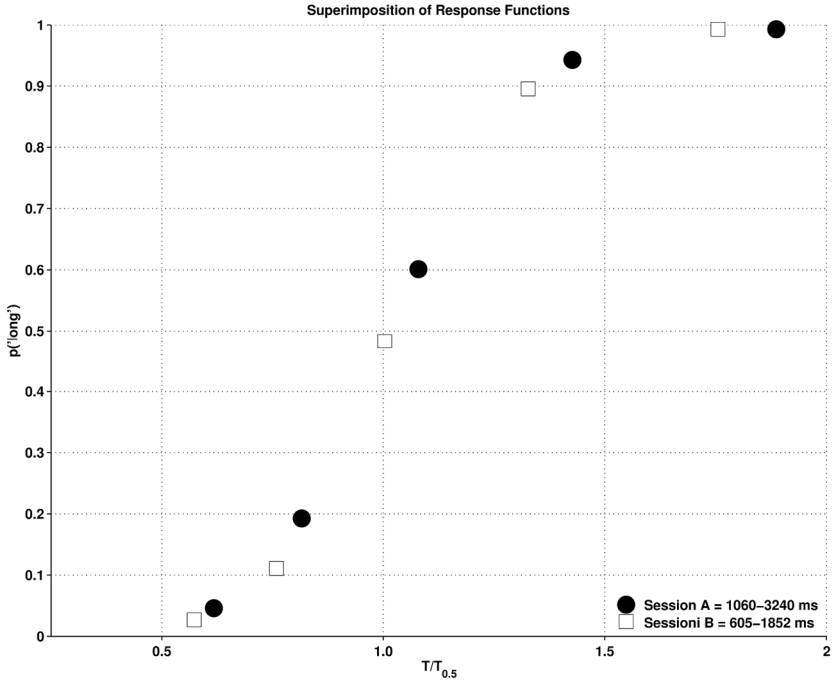


Figure 4.2. Superimposition of the duration classification patterns of the two sessions conformed to the scalar property for time. The values of the probe durations in a given session were first normalized with respect to the mean PSE (1717 and 1058 ms, respectively), i.e., $T/T_{0.5}$, where T is the probe duration, $T_{0.5}$ is the PSE.

Ex-Gaussian RT

Ex-Gaussian fitting was performed to capture the distribution of RTs. Since the duration ranges used in the two sessions were different and the probe spacing was not linear, we analyzed the two sessions separately. Each analysis included Probe duration as the sole within-subject factors in the One-way repeated measures ANOVA.

For *Mu*, the Probe Duration effect was significant in both sessions, $F(4,60) = 21.26$, $p < .001$, ges = .37 for Session Long and $F(4,60) = 12.42$, $p < .001$, ges = .12 for Session Short (Figure 4.3). Similar to Experiment 1, the Probe at the GM served

as the baseline in the contrast against which each probe duration was compared (Table 4.2). In both sessions, *Mu* was comparable between probe = GM and the probes shorter than GM, while there was a sudden drop in *Mu* once the GM was exceeded.

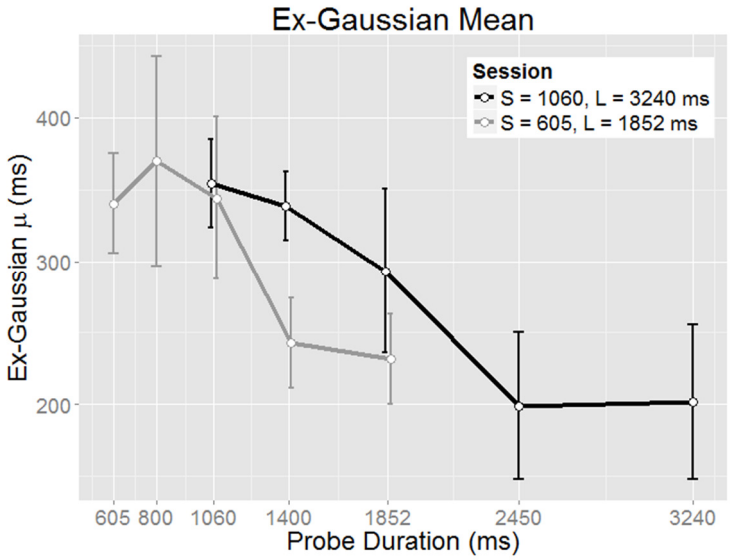


Figure 4.3. Mean ex-Gaussian *Mu* obtained from Session Short (grey) and Long (black). Error bars represent within-subject 95% CI.

Table 4.2

Summary of Contrasts on Ex-Gaussian Mu, using Probe at GM as the Baseline

	Session Long			Session Short		
	coef	t	p val	coef	t	p val
Probe 3 vs. Probe 1	60.96	2.0030	.064	-3.71	-.19	.86
Probe 3 vs. Probe 2	45.26	1.55	.14	25.63	1.079	.30
Probe 3 vs. Probe 4	-94.04	-5.14	.00012	-101.23	-4.40	.00052
Probe 3 vs. Probe 5	-91.46	-5.71	.000042	-112.11	-3.28	.0050

Note: ** indicates statistical significance at α = .013.

For *Sigma*, the Probe duration effect was significant in both sessions, $F(4,60) = 12.23$, $p < .001$, ges = .36 for Session Long and $F(4,60) = 9.52$, $p < .001$, ges = .11 for Session Short (Figure 4.4). Contrasts against the GM probe duration showed that, for Session Long, the RT variability was similar among probes shorter than/ at GM, while there was a sudden decrease once the GM was exceeded. For Session Short, the pattern was similar, but the variability of the shortest probe (605 ms) was marginally smaller than that at GM ($p = .041$; Table 4.3).

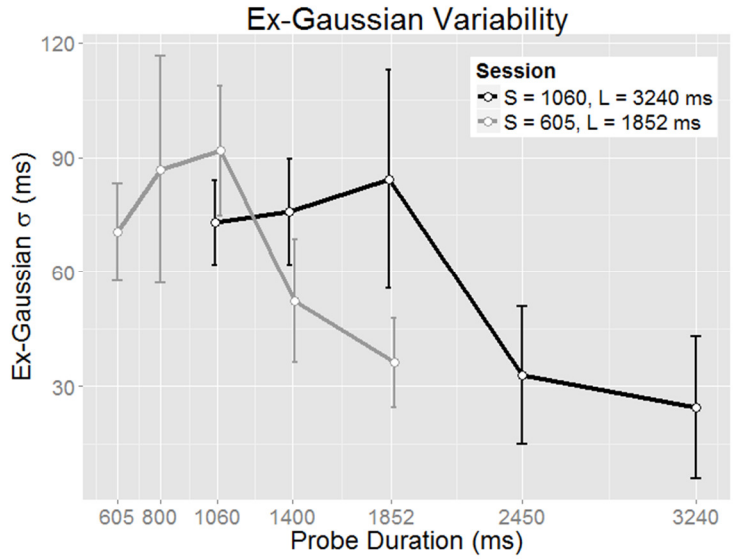


Figure 4.4. Mean ex-Gaussian *Sigma* obtained from Session Short (grey) and Long (black). Error bars represent within-subject 95% CI.

Table 4.3

Summary of Contrasts on Ex-Gaussian Sigma, using Probe at GM as the Baseline

	Session Long			Session Short		
	coef	t	p val	coef	t	p val
Probe 3 vs. Probe 1	-11.33	-.85	.41	-21.43	-2.24	.041
Probe 3 vs. Probe 2	-8.44	-.48	.64	-5.047	-.34	.74
Probe 3 vs. Probe 4	-51.27	-5.26	.000096	-39.46	-4.044	.0011
Probe 3 vs. Probe 5	-59.85	-5.66	.000046	-55.68	-5.35	.000081

Note: ** indicates statistical significance at α = .013.

Finally for *Tau*, the Probe duration effect was significant in both sessions, $F(4,60) = 15.27$, $p < .001$, ges = .28 for Session Long and $F(4,60) = 11.00$, $p < .001$, ges = .24 for Session Short (Figure 4.5). Contrasts against the probe duration at the GM showed that, for both sessions, there were more extreme RTs at the probe = GM than all other probe durations except Probe 4 (2450 and 1400 ms, respectively; Table 4.4).

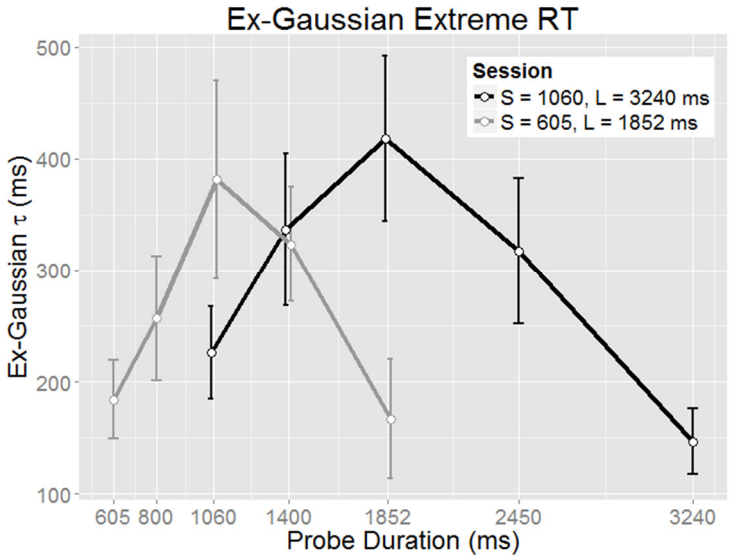


Figure 4.5. Mean ex-Gaussian *Tau* obtained from Session Short (grey) and Long (black). Error bars represent within-subject 95% CI.

Table 4.4

Summary of Contrasts on Ex-Gaussian Tau, with Probe GM as the Baseline

	Session Long			Session Short		
	coef	t	p val	coef	t	p val
Probe 3 vs. Probe 1	-192.21	-4.54	.00039	-197.43	-4.34	.00059
Probe 3 vs. Probe 2	-81.27	-2.72	.016	-124.67	-3.39	.0041
Probe 3 vs. Probe 4	-100.62	-2.015	.062	-58.17	-1.13	.277
Probe 3 vs. Probe 5	-271.34	-6.78	.0000062	-214.87	-4.14	.000876

Note: ** indicates statistical significance at α = .013.

The results from the RTs therefore suggest that participants responded similarly to probe durations shorter or at the GM in most trials, but much faster and less variable once the GM was exceeded. There were also more extreme RTs at probe durations closest to the GMs. These results are consistent with Experiment 1.

ERP Component Verification

Again, the first EEG analysis was done to confirm the presence of the major ERP components (Koenig & Melie-García, 2010), this time with earlier components as well given the chance to compare between sessions. Since the probe durations were carried by auditory tones, these included the auditory evoked potentials (AEP) P1 (0-80 ms), N1 (80-130 ms), P2 (130-260 ms), as well as the bisection CNV (260ms to respective probe durations, i.e., Session Long: 1060, 1400, 1852, 2450, 3240 ms;

Session Short: 605, 800, 1060, 1400, 1852 ms). As before, the boundaries of the time windows were derived from the global field power (GFP) using the subject average ERPs from all epochs regardless of probe duration from Session Long. Figure 4.6 shows the grand average ERPs collapsed across six fronto-central electrodes (FC1/FCz/FC2 and C1/Cz/C2) for each probe duration and session. It can be seen that the CNV appeared to be sharper and more negative in Session Short.

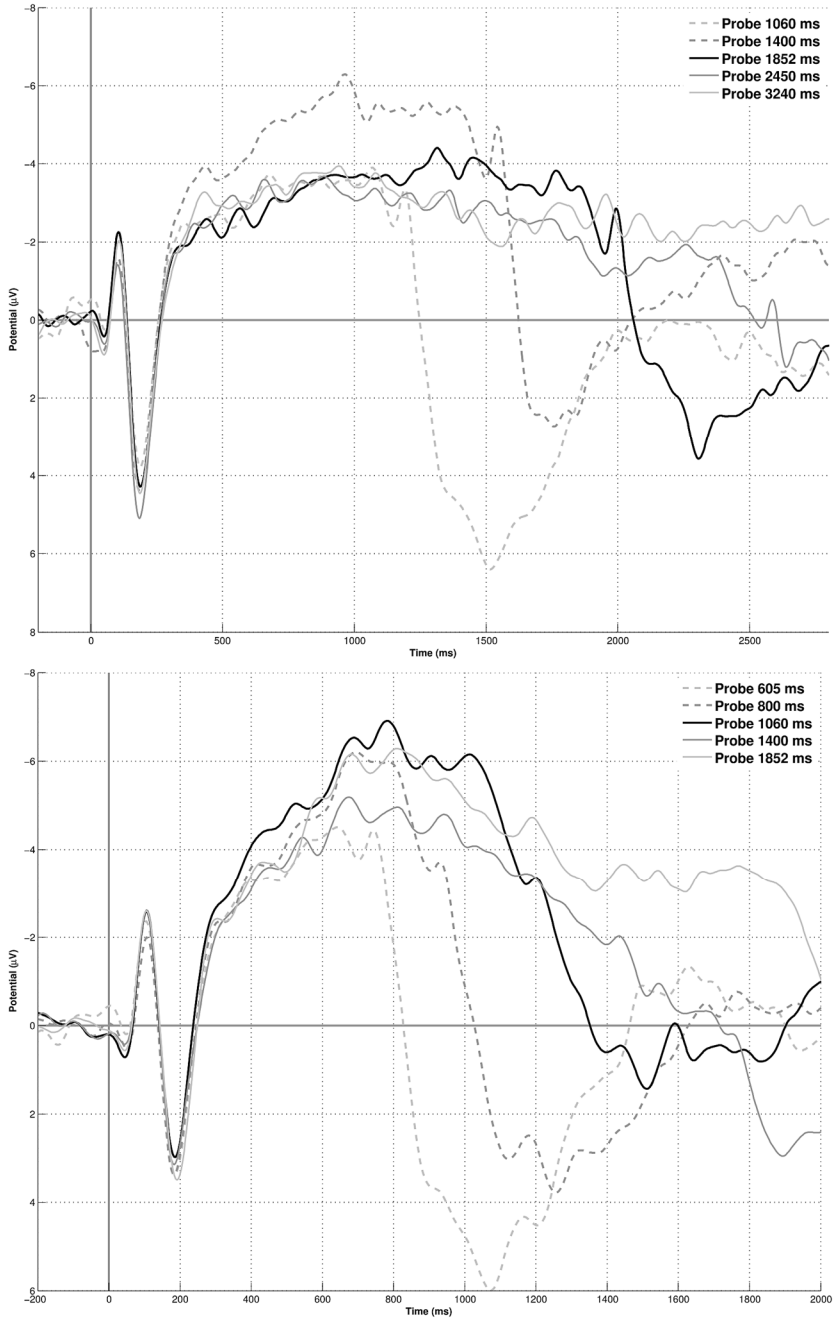


Figure 4.6. Grand average ERPs at fronto-central region for each probe duration for the Long (top) and Short (bottom) sessions, smoothed by 8-point sliding Gaussian windows. Y axis us from 6 to -8 uV, with negativity plotted up.

Mean amplitudes of each ERP component were computed from nine central electrodes (FC1/FCz/FC2, C1/Cz/C2, and CP1/CPz/CP2), where projections of AEP are maximal (Crowley & Colrain, 2004; Wiener et al., 2012). For CNV, the fronto-central electrodes were chosen (FC1/FCz/FC2, C1/Cz/C2). These means were then subjected to one-sample *t*-tests against zero voltage. For the AEPs, each component was observed with their respective polarity from the grand average ERPs (positive/negative/positive). A Two-way repeated measures ANOVA with Session and Component as within-subject factors yielded a significant Session x Component interaction, $F(2,30) = 4.59$, $p = .028$, ges = .018 (Figure 4.7). Paired-sample *t*-tests between sessions suggested a less positive P2 for Session Short, $t(15) = 2.81$, $p = .013$. For the CNV, all probe durations elicited strong negative potentials at central electrodes, as indicated by negative 95% CIs excluding zero (Figure 4.8).

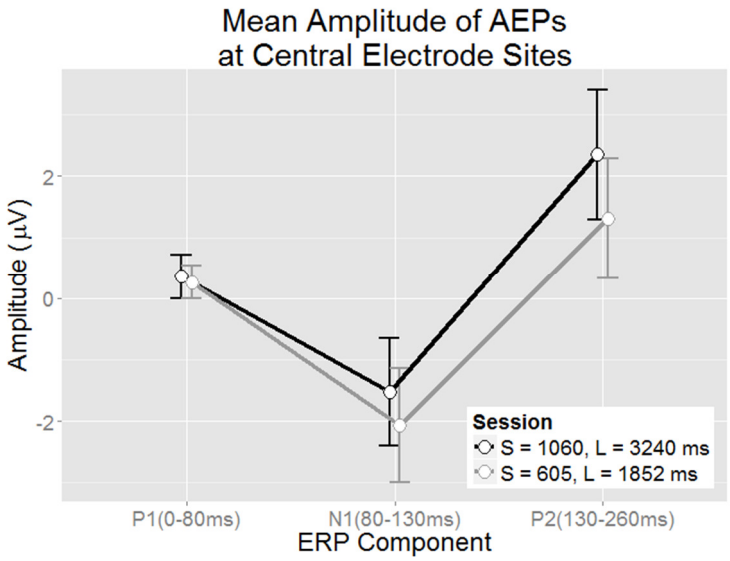


Figure 4.7. Mean amplitudes of the AEPs in the Long (black) and Short (grey) sessions. Error bars are between-subject 95% CIs.

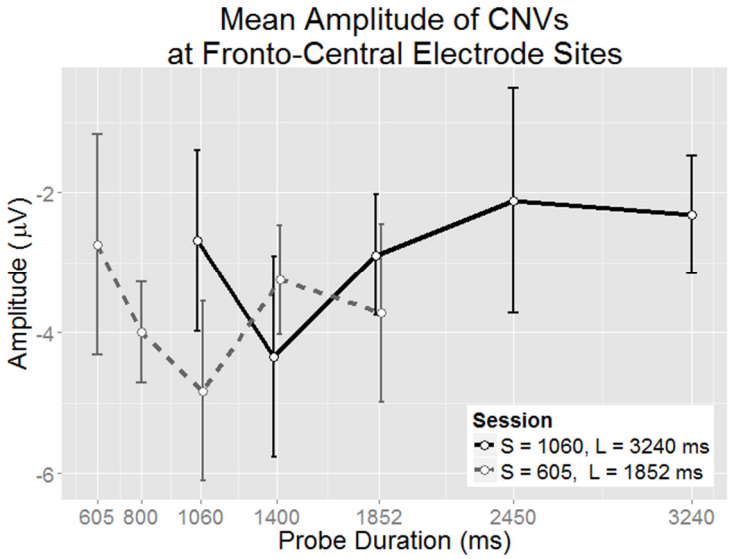


Figure 4.8. Mean CNV amplitudes of different probe durations for the Long (black) and Short (dotted grey) sessions, all measured from 260 ms after stimulus onset, with x-axis representing Probe Duration. The upper limit of y-axis indicates zero microvolts. Error bars represent between-subject 95% CIs.

Early Time Course of the CNV

Analyses of the early CNV time course address the possible relationship between the location of the initial CNV peak (or the first moment the CNV reached a negative plateau) and the short anchor duration, as well as the replicability of the correlation between PSE and the CNV ramp found in Experiment 1. Epochs from the three longest probe durations (i.e., 1852, 2450 and 3240 ms for Session Long and 1060, 1400 and 1852 ms for Session Short) were used to generate the subject average ERPs. The epochs from the two shortest probes were not used because they were close to the short anchors and might confound the peak selection procedure. Subject average ERPs averaged across six FC/C electrodes (FCz/FC1/FC2, and Cz/C1/C2) were then smoothed with a moving window of 100 ms (cf. Pfeuty et al., 2003; Figure 4.9). The comparison of the peak latencies between sessions was done using the jack-knife procedure, which obtains more reliable estimates of peak measures from grand averages than subject averages (Miller, Patterson, & Ulrich, 1998; Ulrich & Miller, 2001). For each session, a jack-knife estimate of the latency was obtained from the grand average ERP computed by leaving one participant out. Each participant was

omitted once, resulting in sixteen jack-knife estimates per session. The peak latencies obtained were 898 ms and 777 ms for the Long and Short sessions, respectively. Jack-knife statistical inference (Miller et al., 1998; Smulders, 2010) suggests that the peaks could not be reliably separated between sessions, $t(15) = .35$, $p = .93$.

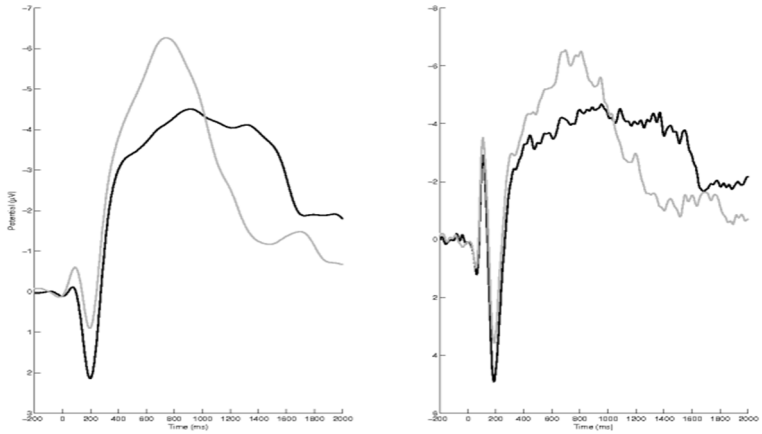


Figure 4.9. Grand average ERP at FCz smoothed with 100ms sliding window (left) and without smoothing (right) for Session Long (black) and Short (grey). Epochs from the two longest probe durations of each session were included in the respective grand averages.

What is also obvious in Figure 4.9 is that the CNV ramp in Session Short was more rapid than that in Session Long. This was verified by computing the CNV initial ramp as the amplitude slope between 260 ms and the respective peak latencies identified with the jack-knife procedure. The slopes for Session Long and Short were -.0048 uV/ms and -.0078 uV/ms, respectively, which differed significantly, jack-knife $t(15) = 3.29$, $p = .0059$, indicating a steeper slope in Session Short.

Following Experiment 1, the same time windows were used to obtain the CNV slopes from subject average ERPs. They were then subject to Pearson correlation analysis. These individual slopes did not correlate with the participants' PSE, $r_{Long} = .34$, and $r_{Short} = .013$, respectively.

Finally, we superimposed the ERPs generated from all epochs in Experiment 1 (S= 800 ms, L = 3200 ms) and those generated from all epochs in Session Long (S = 1060 ms, L = 3240 ms). If the CNV ramp corresponded to the short anchor, we

expected the two slopes to show discernable differences of a 260 ms gap between the short anchors despite a between-subject comparison. When the data between -200 ms and 800 ms were subject to PLSC, there seemed to be amplitude differences for the P200 and the CNV ramp (Figure 4.10), but the latent variable did not reach significance, $p = .30$.

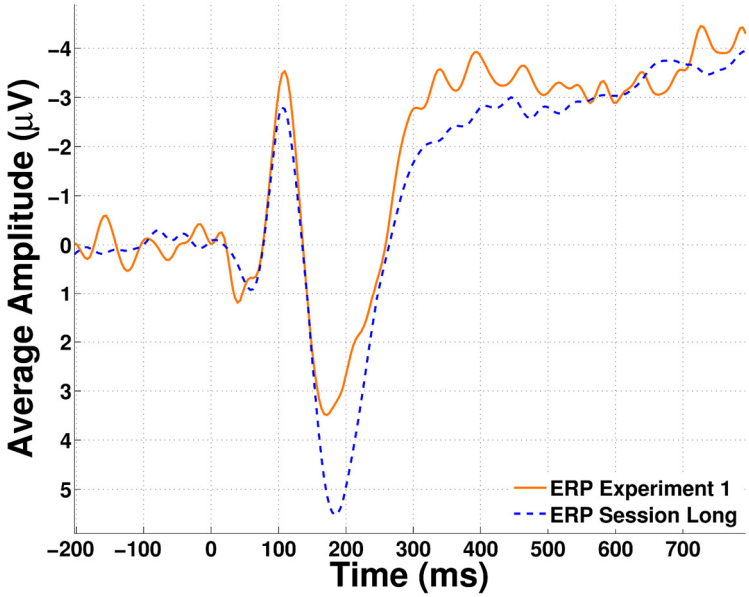


Figure 4.10. Grand average ERP from all epochs in Experiment 1 (solid) as compared to that in Session Long (dotted) at Cz. The rate of change of the CNV amplitude between 250 – 800 ms can be seen to be quite similar, despite use of different short anchor durations (800 and 1060 ms, respectively).

Taken together, while the peak latency of the early CNV was later in Session Long than in Session Short, as indicated by the numerical estimates in the jack-knife procedure, the shift was not statistically different between sessions. A between experiment comparison also did not indicate the early peak of the CNV was sensitive to S, despite the two short anchors differing by 260 ms. On the other hand, the CNV ramp was more rapid in Session Short, in line with pacemaker-accumulator model predictions. However, there was no reliable relationship between the ramp and PSE.

Late Time Course of the CNV

Analyses of the late CNV time course addressed whether the CNV amplitude was constant regardless of absolute duration, suggestive of a fixed neural threshold of

the accumulator (Pfeuty et al., 2005), as well as to replicate the relationship between CNV resolution and the bisection criterion reported in Experiment 1. Epochs from the two longest probes (2450 and 3240 ms for Session Long, and 1400 and 1852 ms for Session Short) were used to generate the subject average ERPs. Figure 4.11 shows the grand average ERPs collapsed across six fronto-central electrodes. The CNV was more negative and peaked in Session Short and it resolved before the presumed bisection criterion (1060 ms). For Session Long, the CNV was sustained and showed a mild dip after the bisection criterion (1710 ms), although there appeared to be a slow gradual decrease in amplitude from much earlier in stimulus presentation.

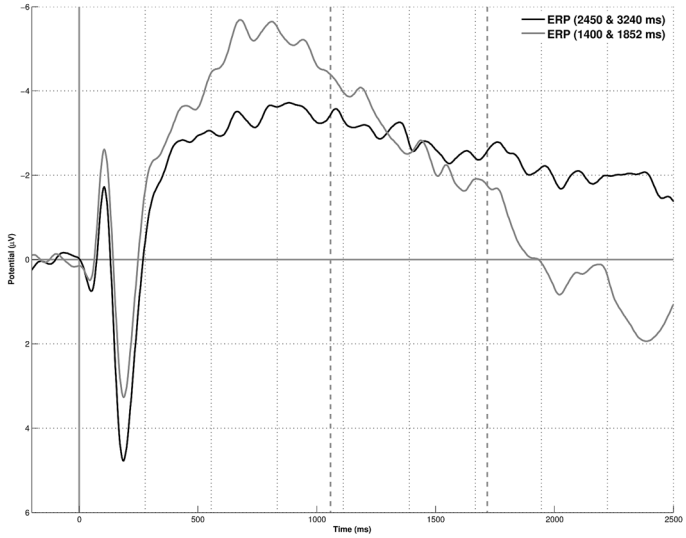


Figure 4.11. Grand average ERPs at fronto-central sites in Session Long (black) and Short (grey), smoothed by 8-point sliding Gaussian windows. Vertical dotted lines indicate the group mean PSEs (1060 and 1710 ms).

Statistical analyses were performed on the CNV slopes, computed on averaged potentials across six FC/C electrodes (FC1/FCz/FC2 and C1/Cz/C2) by regressing voltage on time point, within time windows of interest. The time windows were constructed with size relative to the difference between the AM and the PSE, i.e., 433 ms for Session Long and 170 ms for Session Short. These time windows were positioned relative to the PSE, such that they encompassed two time windows preceding the PSE, one from the PSE to the AM, and the last one after the AM. For Session Long they were 851-1284 ms, 1284-1717 (PSE) ms, 1717-2150 (AM) ms,

and 2150-2583 ms; for Session Short they were 720-890 ms, 890-1060 (PSE) ms, 1060-1230 (AM) ms, and 1230-1400 ms. These slopes were then tested against zero using one-sample *t*-tests. For Session Long, there were positive slopes before the PSE was reached, and the increase in positive amplitude continued afterwards (Table 4.5). For Session Short, there was a marginally positive slope after 890 ms (Table 4.6). The decrease from PSE to AM was not statistically significant. The results in general suggest that the decrease in CNV occurred earlier than that indicated by the PSE and RT pattern.

Table 4.5

Summary of CNV Slopes at Each Time Window of Session Long

Time window (ms)	Slope (μV/ms)	95% CI	one-sample *t*	p val
851-1284	.0017	-.0018, .0053	1.039	.32
1284-1717	.0021	-.00016, .0041	2.30	.036*
1717-2150	.0022	-.00008, .0043	2.21	.043*
2150-2583	.0019	-.00057 - .0044	1.65	.012*

Note: * indicates significance at α = .05

Table 4.6

Summary of CNV Slopes at Each Time Window of Session Short

Time window (ms)	Slope (μV/ms)	95% CI	one-sample *t*	p val
720-890	-.0008	-.0065, .0049	-.30	.77
890-1060	.0054	.00005, .011	2.15	.048*
1060-1230	.0020	-.00032, .0072	.84	.41
1230-1400	.0078	-.00060, .016	1.98	.067

Note: * indicates significance at α = .05.

We then performed the analysis on mean CNV amplitude as well, by creating four 200 ms time windows centered at each of the first four probe durations (Figure 4.12). Subjecting the data to a One-way repeated measures ANOVA, this yielded a significant main effect for Session Long, $F(3,45) = 4.34$, $p = .009$, ges = .04, as well as Session Short, $F(3,45) = 9.42$, $p < .001$, ges = .13. Using the time windows at the probe GMs as the baseline, the contrasts showed a continuous decrease in negative amplitude before the GM in both sessions (Table 4.7), with the changes in Session Long being marginally significant. The mean amplitude at the time window after the GM was not different from that at the GM in Session Long, but was more positive

than at the GM in Session Short. Overall the results are consistent with the slope analysis, showing the CNV resolving earlier than the GM, and the resolution was more gradual in Session Long.

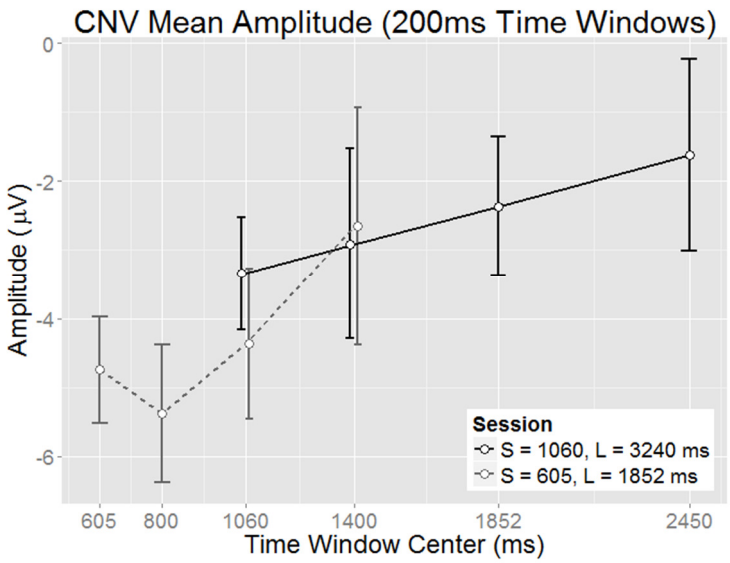


Figure 4.12. Summary of mean CNV amplitude in Session Long (black) and Short (dotted grey) at each time window. Error bars represent between-subject 95% CIs.

Table 4.7

Summary of CNV Mean Amplitude Contrasts with the Probe = GM as Baseline

	Session Long				Session Short		
	coef	t	p val		coef	t	p val
1060 ms	-.98	-2.093	.054	605 ms	-.38	-1.14	.27
1400 ms	-.54	-1.98	.066	800 ms	-1.014	-2.55	.022*
2450 ms	.75	1.69	.11	1400 ms	1.71	3.25	.0054*

Note: * indicates significance at α = .05

Taken together, the changes in CNV slope and mean amplitude across time windows indicate a more peaked and negative CNV when anchor durations were short (i.e. Session Short). When a CNV resolution was observed (weakly in CNV slope for Session Long, both in slope and amplitude for Session Short), it happened earlier than the PSE/GM.

The CNV Amplitude as the Clock Threshold

To check whether the 'threshold' of the CNV was fixed regardless of anchor duration, as expected based on previous studies of explicit timing (e.g., Pfeuty et al.,

2005), implicit motor timing (Praamstra et al., 2006), and temporal anticipation (Ruchkin et al., 1986), we first obtained the ERPs from epochs of the two longest probe durations, receiving a Long response, in each session. We defined threshold in two ways. First, we assumed it to be at the PSEs, because as discussed in Chapter 2 it is the bisection criterion (cf. Ruchkin et al., 1986). The mean CNV amplitude, averaged across six fronto-central electrodes, in 200ms time windows preceding the PSEs (1517 – 1717 ms for Session Long, and 860 – 1060 ms for Session Short) were obtained for each participant. A permutation paired-sample *t*-test yielded a significantly more negative CNV amplitude in Session Short, $t(15) = 2.49$, $p = .0033$. We then assumed another threshold, defined as the latency of the maximum CNV amplitude, which was found in the jack-knife procedure (898 and 777 ms). Time windows of 200 ms were constructed centered at each maximum to obtain the mean amplitudes. Not surprisingly, a permutation paired-sample *t*-test again yielded significantly more negative amplitude in Session Short, $t(15) = 4.00$, $p = .0013$.

CNV Amplitude and Subjective Time

Similar to Experiment 1, PLSC was used to identify potential differences between the ERPs from trials classified as Short (RS) and Long (RL), separately for each session. Since there were more trials per probe duration in Experiment 2 (90 trials), and the spacing between probes was larger, the ERP data from the probe duration with p('long') nearest to .5 were selected for each participant. For participants who showed abrupt changes in p('long') (e.g., from .25 to .75), the probe with the larger p('long') was selected. Separate PLSCs were performed on subject average ERPs time-locked to the probe onset and probe offset for each session, resulting in four (2 time-lock x 2 sessions) analyses. For onset-locked data, the analysis time window was -200 ms to the GM (1852 and 1060 ms) of the respective session. For offset-locked data, the analysis time window was -200 to 800 ms. PLSCs

were also conducted on the time-frequency transformed data of the onset-locked EEGs.

Onset-locked data of Session Long. Consistent with Experiment 1, none of the PLSCs of the four analyses yielded significant LVs based on permutation results. For the onset-locked data from Session Long, LV1 attained a *p* value of .13, although electrode salience was predominately positive, indicating that RL is more negative than RS in general (Figure 4.13). Applying a permutation paired-sample *t*-test to the difference also did not yield significance either, $t(15) = 1.36$, $p = .20$.

Onset-locked data of Session Short. For the onset-locked data from Session Short, LV1 attained a *p* value of .23. Electrode salience was positive (RL more negative) at frontal sites at the P1-N1 time window (44-106 ms) and negative at occipto-parietal sites as time approached 1060 ms (RS more negative; Figure 4.14).

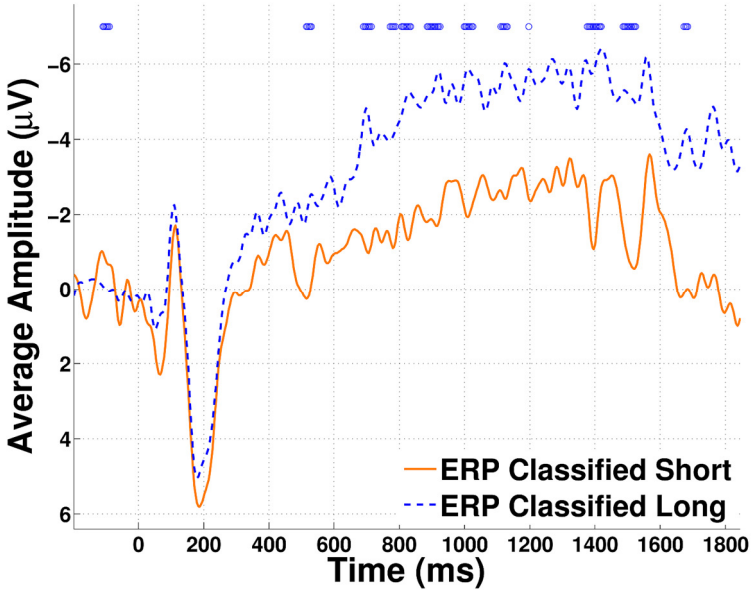


Figure 4.13. Onset-locked grand average ERPs from trials classified as Short (solid) and Long (dotted) at electrode CPz in Session Long. ERP of Long responses was more negative than Short responses, but the latent variable was not significant. Stable salience (bootstrap ratio > 2.00) is marked with empty circles at the top of the panel.

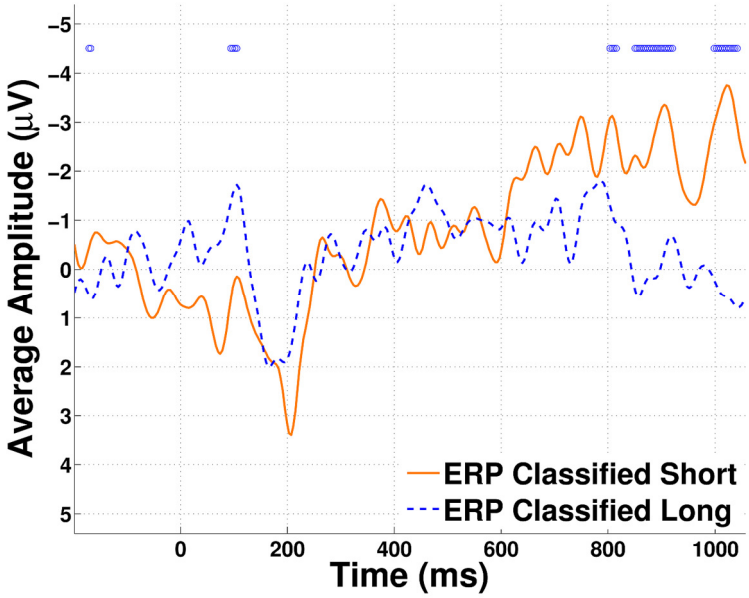


Figure 4.14. Onset-locked grand average ERPs from trials classified as Short (solid) and Long (dotted) at electrode POz in Session Short. ERP of Long responses was more negative than Short responses early in the trial, and vice versa as time proceeded. However, the latent variable was not significant. Stable salience (bootstrap ratio > 2.00) is marked with empty circles at the top of the panel.

Offset-locked data. If the offset component is sensitive to the bisection criterion, because it was found to be larger before the criterion was reached in Experiment 1 (cf. Lindbergh & Kieffaber, 2013), we expect it to be more positive to trials classified as Short, despite identical probe durations. For offset-locked data from Session Long, LV1 attained a *p* value of .094 and was not significant, although stable salience after probe offset showed a parietal distribution and was more positive when trials were classified as Short than Long, consistent with the results of Experiment 1 (Figure 4.15 left). On the other hand, the difference between offset components was significant in Session Short, with the LV attaining a *p*-value of .002 and showing similar parietal focus (Figure 4.15 right).

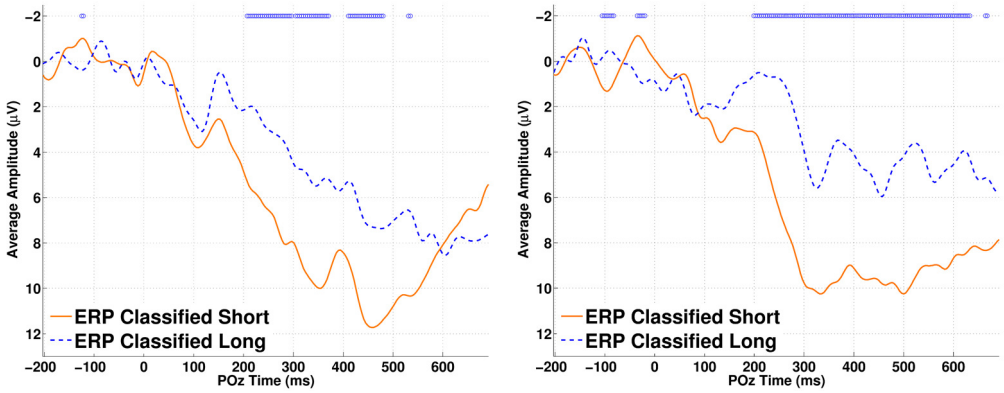


Figure 4.15. Left: Offset-locked grand average ERPs from trials classified as Short (orange) and Long (dotted blue) at electrode POz in Session Long. ERP of Short responses was more positive than Long responses after the duration offset. However, the latent variable was not significant. Right: the same set of ERPs in Session Short, showing similar pattern, but this time the latent variable was statistically significant. In both panels, stable salience (bootstrap ratio > 2.57) is marked with empty circles at the top of the panel.

CNV Differences between Sessions

To explore what cognitive processes may account for this difference in the CNV amplitude, the subject average ERPs from the probe durations present in both sessions (1060, 1400 and 1852 ms), were submitted to PLSC analysis. All epochs from these probes were averaged together to generate the subject average ERPs. Only common time points between -200 to 1060 ms were analyzed (df = 1). The latent variable (LV) was statistically significant, $p = .01$. Stable salience was recorded at 410 to 1030 ms, with Session Short being more negative at central sites slightly lateralized to the right (Figure 4.16). This result essentially replicated the analysis performed earlier regarding the CNV as decision threshold.

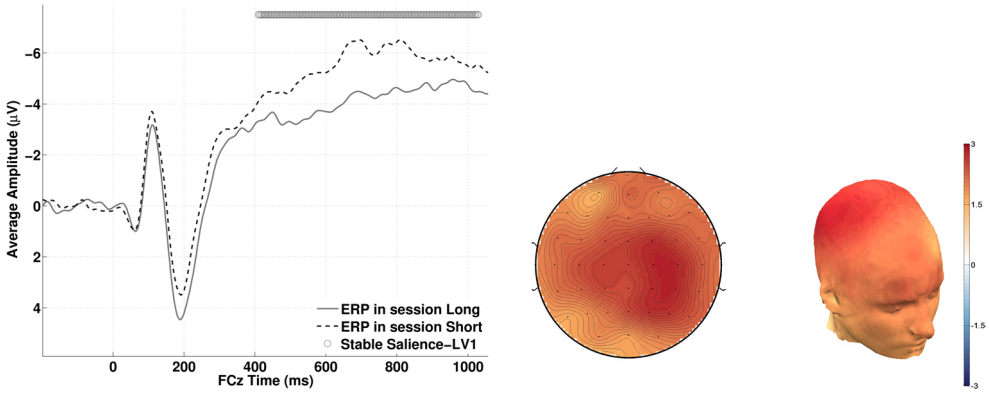


Figure 4.16. Left: Onset-locked grand average ERPs from Session Long (Solid grey) and Session Short (Dotted grey) at FCz. Stable salience (bootstrap ratio > 2.57) is indicated with empty circles at the top of the panel. Right: The topographical distributions of the fronto-central salience at 410-1030 ms, with positive salience (red) indicating larger positivity in Session Long.

PCA. To better understand what this difference in CNV amplitude may represent, we performed Principal Components Analysis (PCA) on the ERPs of onset-locked data. To reduce volume conduction so that better topographical maps can be discerned for each PC, we first applied CSD to the ERP at each electrode for each participant in each condition. The CSD transformed data was then subject to PCA (Kayser & Tenke, 2003). Both sessions were included in one decomposition. The first four PCs explained 85% of the covariance. Of interest is the first PC, which explained 69.83% of the covariance (Figure 4.17).

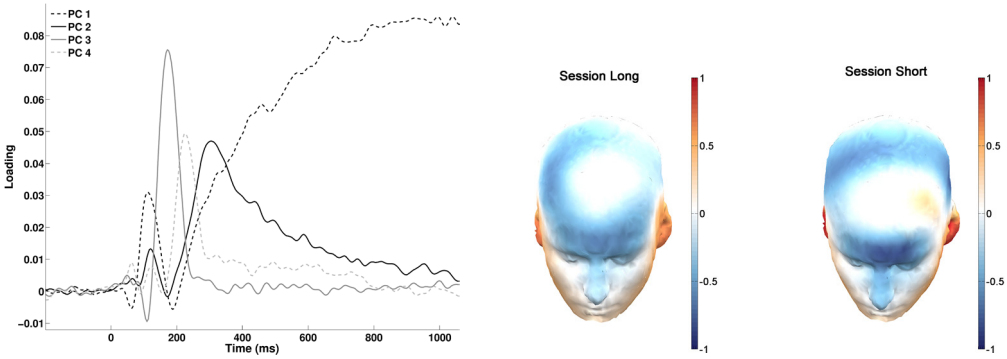


Figure 4.17. Left: Loading of the first four principal components (PCs). Right: Topographical distributions of PC 1 in Session Long (left) and Short (right).

PC 1 captured the sustained negativity. Its factors scores gave a topographical distribution that was along the premotor area on both hemispheres, which was stronger in Session Short than session Long. To confirm this visual impression, the factor scores at FC3/FC5, C3/C5, FC4/FC6, and C4/C6 were averaged into two regions of interest (ROI) onefor each hemisphere. The data was then subject to a Two-way repeated measures ANOVA with Session and ROI as the two factors. This yielded significant main effect of Session, $F(1,15) = 7.20$, $p = .017$, ges = .056 (Figure 4.18). The bilateral activity was close to the auditory cortices in the temporal lobe and/or the motor area for the hands, suggesting that the larger CNV negativity in Session Short might be due to perceptual enhancement (Hillyard, Vogel, & Luck, 1998) or motor-related processes that is consistent with a response uncertainty hypothesis (Tecce, 1972). It is also noted that PC 2 (black in Fig. 4.17), which explained 6.76% of covariance, had a fronto-central distribution, consistent with that of the CNV; however, it peaked very early (before 400 ms), well before the short anchors and PSEs. Thus, although the CNV, with volume conduction, showed a difference in amplitude at slightly right lateralized central sites, this difference may originate from differences in the bilateral sustained activity.

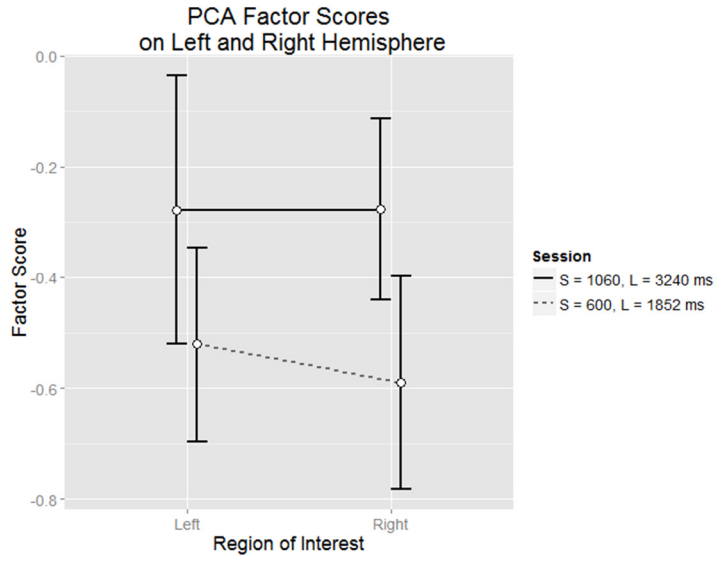


Figure 4.18. Mean factor scores, which indicate the strength of PC2 at each electrode site, as a function of ROI (region of interest) and Session.

Positive Component at Duration Offset

Finally, we again looked at the offset component to replicate the results of Experiment 1. All the epochs were averaged separately according to probe durations, time-locking to the probe offset, separately for each session. The baseline of the epochs was set to be the 200 ms pre-stimulus offset. The data was then subjected to PLSC analyses (df = 4 each). In both sessions, LV1s were statistically significant, *p*s < .001, and explained 77.8 and 79.5% of the covariance, respectively. As the brain scores show (Figure 4.19), the change in the amplitude of the positive component is similar to that observed in Experiment 1, with the decrease in amplitude at and after the probe = GM (1852 and 1060 ms, respectively).

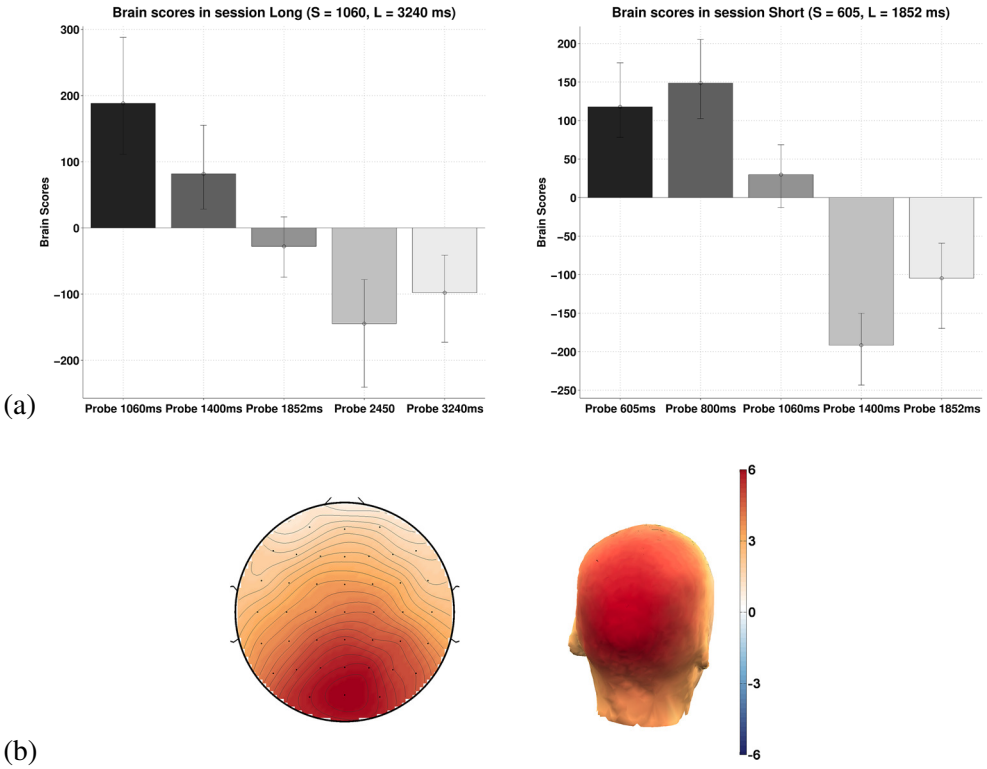


Figure 4.19. (a) Brain scores as a function of probe durations in Session Long (left) and Short (right). There is a sharp change in sign in the scores after probe GM (middle grey bar in each panel), indicating a large decrease in the amplitude of the slow positive wave. (b) Topographical distribution of the latent variable between 250 and 555 ms (bootstrap ratio > 2.57), with a parietal focus. The data is from Session Long, but it is representative of both sessions.

Discussion

Experiment 2 served to examine the predictions made under the pacemaker-accumulator model, but which could not be tested with only one duration range, i.e., that the two CNVs should share similar maximal negativity, while the CNV ramp in the session with shorter anchors should be steeper than that with longer anchors. Since two short anchors and GMs were involved and the two bisection tasks were controlled for difficulty, the CNV early peak and late resolution should shift accordingly. In addition, analyses were conducted to replicate the relationships between the CNV time course and the short anchor and bisection criterion found in Experiment 1.

Results showed that the CNV amplitude was more negative in the sessions with shorter absolute durations. The shape of the CNV also seemed to differ between sessions. As shown by the PCA analysis and further detailed below, these observations are more consistent with processes such as temporal attention than a pacemaker-accumulator process. Furthermore, the relationships regarding the CNV peak and/or resolution were at best partially replicated.

The Bisection Criterion

The behavioral data regarding the bisection criterion is largely consistent with Experiment 1. Analyses of the PSE showed that participants performed according to the magnitude of the anchor durations used, with the PSE in Session Long being longer than Session Short. One unexpected exception is that the mean PSE in Session Long was shorter than the GM by 140 ms, which was marginally significant. A Bayesian approach with BIC approximation (Masson, 2011) yielded p(PSE not equal 1852|data) = .68, or a Bayes factor of .47, which represents weak evidence against the null hypothesis. Since a similar number of different probes (five, but all shorter than 1000 ms) was used in Allan (2002a) to yield a PSE near the GM, and no such shift was observed in Session Short, we do not have a ready explanation for the shortened PSE. The sparse spacing between probe durations might have made the bisection task

easy and greatly shortened the perception of L due to memory mixing, leading to a shortening of the PSE (Klapproth & Wearden, 2011).

The WF was the same between sessions, demonstrating the scalar property of duration estimation in the bisection task. The value of WF (.16 and .14) was also comparable to that obtained in other studies, indicating satisfactory performance. It also indicates that performance in the two sessions was comparable on temporal variability. We argue that this implies comparable difficulty of the two bisection tasks. Finally, the ex-Gaussian analysis on the RTs gave similar results as in Experiment 1, with probes near the PSE giving the largest *Tau*.

CNV Time Course Reflects Critical Durations

The finding that the CNV resolved at the PSE in Experiment 1 was at best only partially replicated in Experiment 2, because the morphology of the CNV was considerably different between sessions, and the latency of the CNV resolution did not match reliably with the PSE in either session. Regarding the early time course of the CNV, the initial CNV slope was steeper when the anchor durations were shorter, as identified by the jack-knife procedure. This is consistent with pacemaker-accumulator models that assume a fixed decision threshold (Pfeuty et al., 2005; Simen et al., 2013). For example, Simen et al. (2013) discussed the neural plausibility of their adaptive pacemaker-accumulator model and surmised that the neural activation as threshold is the limiting factor of a cognitive model because neural firing rate is bounded. Instead, timing different durations with a fixed threshold at close to maximal neural activation, but with an adjustable rate of temporal evidence accumulation is more feasible. The direction of difference in slopes observed here is consistent with this kind of pacemaker-accumulator model. However, unlike Experiment 1, the correlation between this initial slope and the PSE was not significant. These results are partially supportive of the pacemaker accumulator model, although not strong support.

Furthermore, although the early peak of the CNV in Session Long was numerically later than that in Session Short, the jack-knife analysis failed to indicate that they were different. As shown in previous literature, the CNV peak was sensitive enough to indicate smaller differences in criterion and when the criterion was shorter than 800 ms (e.g., 149 and 600 ms, respectively in Pfeuty et al., 2005). So, support for the hypothesis that the initial CNV peak reflects the duration of the short anchor was mixed.

Regarding the late time course, the slope and mean amplitude analyses revealed CNV resolution earlier than the PSE. At the GM, the change in CNV slope was mild at best. This weaker manifestation of the short anchor and bisection criterion in the CNV may be due to the small number of probe durations, so that the difficulty of the task was decreased (Paul et al., 2011), good performance could be maintained even with fuzzier representation of the bisection criterion. Also, the binary assignment of response may have blurred the anchor representations (Droit-Volet & Izaute, 2009).

Early peaking of the CNV has been reported previously. As mentioned in the Introduction, Ladanyi and Dubrovsky (1985) found that better timers showed smaller CNVs and earlier CNV resolution. Studying target detection at threshold with the S1-S2 interval (ISI) fixed at either 1, 3, or 6 seconds, Loveless (1975) reported similar morphologies of a negative slow wave as in our study: fronto-central distribution, peaking at about 1000 ms regardless of ISI, and more negative when ISI was 1 second. Loveless regarded this negativity as the CNV and attributed its role to S1 orientation, such that neural excitability is increased for more efficient processing and response to the upcoming S2 (Birbaumer et al., 1990; Funderud et al., 2012). Filled signals, also used here, were more effective in facilitating anticipation (e.g., Simons, Huffman, & Macmillan III, 1983). This non-correspondence between the peak of an electrophysiological component and timing or temporal anticipation was also recently

illustrated by Fujioka, Trainor, Large, and Ross (2012) with a vastly different task using MEG. Participants passively listened to rhythmic or random tone sequences. The inter-tone interval (ITI) was parametrically varied from 390, 585, to 780 ms in separate blocks. Beta power desynchronization (13-30 Hz) was strong in all rhythmic and random conditions. While the initial drop in beta power (akin to the CNV ramp here) and the latency of the minimal power in the rhythmic condition did not vary as a function of ITI in any condition, the rate of rise of the power from this trough to baseline beta power was slower as the ITI increased in the rhythmic conditions. While the magnitude of the duration, the nature of the signal (MEG instead of EEG), and the neural origin of the beta changes (auditory cortices) differed from the current study, beta power has been shown to reflect interval timing at the hundreds of milliseconds to seconds range in an MEG study (Carver, Elvevåg, Altamura, Weinberger, & Coppola, 2012), and the correspondence between CNV resolution, but not at the peak latency, has been suggested before (e.g., at the zero-crossing, Pouthas, Garnero, Ferrandez, & Renault, 2000).

CNV as the Temporal Decision Threshold

Several groups have proposed that the CNV amplitude may reflect a decision threshold. For instance, Ruchkin et al. (1986) posited that to qualify as an index of expectancy, the maximal CNV negativity by the time of S2 occurrence should be independent of the S1-S2 latency, as confirmed in their experiment using 1 s and 3 s foreperiods. More recent studies using explicit (e.g., Pfeuty et al., 2005) and implicit timing (Mento et al., 2013; Praamstra et al., 2006) tasks also observed relatively constant CNV amplitude when the change in criterion time was of tens to hundreds of milliseconds. But the mean amplitude analysis and PLSC showed that the CNV was always more negative in Session Short than Session Long, which does not support a pacemaker-accumulator interpretation. Furthermore, if one interprets the CNV in a timing task as reflecting the accumulator, or the magnitude of the neural

representation of time, the more negative CNV in Session Short would suggest that shorter durations were represented by larger CNV negativity, an observation in contrast to Macar et al.'s (1999) findings.

It has been shown that the CNV amplitude may not reflect the decision threshold per se, but the distance between the starting point of an accumulation process and its threshold, sometimes referred to as response caution (Forstmann et al., 2008). The larger the distance, the more evidence must be accumulated, and the higher accuracy, but longer reaction time to the imperative stimulus. Specifically, this distance would be expected to be short under speed instructions as compared to accuracy instructions. In a non-temporal dot motion detection task, participants were asked to focus on accuracy or speed when trying to detect the direction of the motion of randomly distributed dots on the computer screen (Boehm et al., 2012). EEG data of the CNV measured between a fixation cross and before the onset of the dot kinematogram was fitted with two parameters from the Linear Ballistic Accumulation Model (LBA, Donkin, Brown, & Heathcote, 2011; Forstmann et al., 2008), one of which was response caution. Single trial CNV amplitude was predicted by response caution, but only in the speeded condition. The effect on CNV by a normal instruction such as we gave was found to be more similar to a speed instruction than an accuracy condition (cf. Loveless & Sanford, 1974). However, since the same instruction was given in each session, the instructional effect should be the same. If time perception is achieved through accumulation of evidence (clock ticks) that is reflected in CNV, these results imply that the CNV amplitude may reflect some initial bias that determines how many more pulses are needed to match the perceived time with remembered target time.

Taken together, these results and those from Fujioka et al. (2012) are not inconsistent with an orienting role of the bisection CNV: the duration onset aroused the participants, triggering a CNV that defines some form of initial starting point,

from which the rate of decrease in the negativity is itself the time estimation or is governed by underlying timing processes. Future study may focus on whether similar predictability of time can be found at the rate of the resolution of the CNV.

CNV Amplitude and Perceived Duration

The amplitude analysis of the CNV between ERPs associated with Short responses (RS) and those with Long responses (RL) again failed to converge with the results of Macar et al. (1999) and Bendixen et al. (2005). The latent variables extracted by PLSC were not statistically significant. Although the mean amplitude of RL was more negative than RS in Session Long, this was not so in Session Short. Even if we inspect the salience stability despite non-significance, stable salience that indicated reliable differences between RS and RL were quite transient with respect to the sustained nature of the CNV. Across two experiments, we cannot rule out a task difference in the failure to replicate. However, given the formation of the criterion time is highly compatible between timing tasks and humans adapt very well to variance in temporal information in a variety of tasks we argue that if subjective time was reflected in the CNV amplitude, it should have also manifested in the duration bisection task.

What the CNV may Reflect

The conformation of the CNV shapes to the Type A/B classification of Tecce (1972) and the bilateral difference in amplitude between sessions found in PCA are broadly consistent with the conjecture that the CNV reflects response uncertainty and/or sustained attention. It ramped and resolved at moments demarcating possible response times, because one had to pay attention to these moments in order to gather enough information for the response (Campbell et al., 2009; Trevor & Tecce, 1998). As absolute time decreased, so did the window of possible response possibility. In addition, certainty of response increased as absolute time decreased (Niemi & Näätänen, 1981) because of the scalar property of time (MacDonald & Meck, 2004),

so that participants could anticipate the offset of the durations more accurately and prepare to respond better. Lower uncertainty may allow cortical excitability to be adjusted more effectively (Gontier et al., 2009; Rockstroh et al., 1991), resulting in more negative CNV, as is often reported in foreperiod studies that the earlier the arrival of the S2/target stimulus the more negative the CNV (McAdam, Knott, & Rebert, 1969; Miniussi et al., 1999). Alternatively, the bilateral distribution of the CSD data in the PCA may indicate that participants paid more attention when absolute durations were shorter because they were better able to anticipate the offset of the durations, so that the sustained auditory processing (also a negative slow wave, cf. Campbell et al., 2009) was modulated (Hillyard et al., 1998; N'Diaye et al., 2004).

Auditory Evoked Potentials

Some differences in the AEPs were observed. First, there was a less positive P2 in Session Short than Session Long. Second, the P1-N1 was less positive in the ERP from trials classified as long than short in Session Short, although the corresponding PLSC analysis was not significant. We do not have ready explanations for these differences. AEPs are known to be sensitive to attentional modulation. For instance, Xuan, Chen, He, and Zhang (2009) asked participants to perform temporal discrimination between pairs of brief durations (600 - 800 ms). The durations were either carried by an Arabic digit that was congruent with the relative length of the duration in the pair (e.g., digit 9 for the longer duration and 1 for the shorter) or incongruent (e.g., digit 1 for the longer duration and 9 for the shorter). ERP analyses indicated that durations paired with small digits were associated with a more negative N1. The authors attributed this effect to the stronger temporal orienting induced by small digits: Participants anticipated earlier arrival of the stimulus offset in these trials, thus more attention resources were allocated in the early portion of the epoch.

The functional implication of the P2 is not well understood (Crowley & Colrain, 2004), but it has been argued to reflect inhibition of perceptual processing

that may interfere with the processing of more important aspects of the stimuli (e.g., Oades, Dittmann-Balcar, Schepker, Eggers, & Zerbin, 1996). Stronger inhibition is related to a more positive P2, although its positivity also increases with age (Crowley & Colrain, 2004). Liu et al. (2013) showed that the P2 increased in positivity as attention devoted to the timing aspect of the stimulus in a dual-task setting increased, which suggests that the level of attention paid to the task may be different between sessions in the current experiment. This might account for the shortened PSE, relative to the GM, in Session Long, but not Session Short. More attention was paid in some trials during Session Long, such that the bisection criterion was reached relatively earlier (e.g., the pulses were accumulated with less loss compared to other trials), leading to more long responses.

The anticipatory explanation of the CNV might help explain the between-session differences in the N1-P1 time window. As shown in Bendixen et al. (2005) using durations shorter than 500 ms, the amplitude difference between the ERP from trials classified as Short and from those classified as Long can occur as early as the N100, as if these components superimposed with an early-onset negative slow wave. While these authors concluded that their results were consistent with the accumulator hypothesis, we argue that these early changes can also be consistent with an attentional account, such that more attention, indicated by the early-onset negativity, was paid in trials eventually classified as long earlier in the trial, such that the duration was more likely to be perceived as longer than the criterion (Brown, 1997).

Offset Positive Component

The slow positive wave observed in Experiment 1 was also seen in Experiment 2. In particular, it was less negative when the probe was classified as Short than Long, despite identical physical duration magnitude. Similar to Experiment 1, the slow wave was much less negative once the probe durations exceeded the GM. While there are considerable experimental and analytical

differences between the current experiment and those by Gibbons and colleagues (2005, 2008) and Lindbergh and Kieffaber (2013), the consistent association of this positivity with the Short identity of the durations involved as well as its modulation by duration magnitude differences invites the interpretation that this ERP component reflects processes due to the comparison between the current probe and the bisection criterion, further supporting the presence of such criterion near the GM.

To conclude, Experiment 2 attempted to clarify the changes of the CNV time course at critical moments during a bisection trial. Unfortunately, the results did not provide strong support for the hypothesis that the early CNV time course reflects the Short anchor, or the late CNV time course reflects the bisection criterion, perhaps due to a decrease in task difficulty. On the other hand, we also showed that a pacemaker-accumulator process cannot satisfactorily explain the changes in the CNV when there was a change in the GM. The CNV was more negative when the bisection criterion was shorter, which may be driven more by a decrease in the response uncertainty due to shortened absolute time.

Chapter 5 Relating CNV Characteristics to the Modality Effect on Perceived Duration

In Experiments 1 and 2, we failed to find any reliable support for the pacemaker-accumulator interpretation of the CNV changes. One may argue that allowing participants to perform the bisection task with minimal instruction may have resulted in large between-subjects variability (different participants had different PSEs), but relatively small within-subjects variability (e.g., differences in subjective time by post-experiment trial classification), rendering the ERP analysis not sensitive enough. In Experiment 3, we tried to induce larger variability in within-subjects perceived time by a manipulation that is argued to tap into the clock mechanism.

Modality Effect on Perceived Time

In the pacemaker-accumulator model, differences in perceived time can arise due to a difference in clock speed or the onset delay of the mode switch connecting the pacemaker and the accumulator between two conditions (Penney, 2003). This is exemplified in the study of timing in different sensory modalities. It is repeatedly demonstrated that that auditory duration is judged longer than its visual counterpart; temporal variability is also smaller in the auditory modality (Goldstone & Lhamon, 1974; Stauffer, Haldemann, Troche, & Rammsayer, 2011; Wearden et al., 1998).

To understand the modality effect on perceived duration, Penney et al. (2000; Penney et al., 1998) asked participants to perform supra-second duration bisection tasks (3-6 s; 2-8 s, 4 -12 s). In their Experiment 1, both auditory and visual anchor durations were presented during the anchor training phase, and probe durations of either a single signal (visual/auditory) or compound signals (asynchronous, overlapping visual and auditory) were presented during the test phase. The durations used were the same for both modalities. Participants were not explicitly instructed which anchors they should compare against. Results showed that the psychometric function of the visual probes was displaced rightward and the visual PSE was further

away from GM/AM than the auditory PSE. These displacements did not occur when the two modalities were trained and tested in separate sessions, or when different anchor durations were used for each modality in the same session (e.g., 3-6 s for auditory and 4-12 s for visual).

According to the pacemaker-accumulator model, modality specific clocks exist, with the auditory clock running faster than the visual clock, thereby representing the same duration with more clock ticks (Ulrich, Nitschke, & Rammsayer, 2006). Penney and colleagues postulated that a memory mixing effect had occurred (van Rijn & Taagten, 2008; Gu & Meck, 2011), in which the representation of the durations of both modalities were integrated into one distribution. For each trial, participants drew a sample from this distribution and compared it with the probe duration, regardless of modality. On average, an auditory duration would comprise more ticks than the criterion, while a visual duration would comprise fewer ticks than the criterion. Hence, the auditory duration would be more likely to be classified as long than its visual counterpart. Since memory mixing could not occur when the two modalities were not in the same experimental block or when their anchor durations were too different, no common referent could be established. Furthermore, their psychometric fitting (Gibbon, 1981) suggested that auditory memory dominated the common referent, so that the visual duration was more affected. They concluded that these results were consistent with a shared timing mechanism across modalities. Gamache and Grondin (2010) reached a similar conclusion regarding the common referent by observing that the visual PSE was further away from the central tendency than was the auditory PSE.

Wearden and colleagues (Wearden et al., 1998; Wearden, Todd, & Jones, 2006) replicated the modality effect in both temporal generalization and bisection tasks using much shorter sub-second time intervals. They also observed that the processing of auditory durations was always less varied. But instead of the clock

speed difference, they attributed this variability difference to the different efficacy of the attentional mode switch, with the auditory switch being less variable and faster to close than the visual switch due to the more automatic nature of auditory processing (Chen et al., 2010). As a result, the onset and offset of the auditory stimulus are registered more accurately, leading to less variable representation of the criterion duration. The superior stability and temporal resolution in auditory perception is consistent with findings in intersensory perception that auditory stimulus often alters the perception of the visual stimulus instead of vice versa (e.g., Fendrich & Corballis, 2001; Jaśkowski, Jaroszyk, & Hojan-Jezierska, 1990).

Regardless of the underlying mechanisms of the modality effect on perceived duration, these findings show that using modality, we may alter the target duration or the criterion time used in the timing task. If the pacemaker-accumulator interpretation of the CNV holds (Macar & Vidal, 2004), then systematic changes in the CNV time course should occur in conjunction with the modality effect. However, if the CNV reflects overall temporal attention or motor preparation, then the bilateral Principal Component (PC) found in Experiment 2 should be replicated and fail to show modality differences.

To this end, we adapted the paradigm used in Penney et al. (2000). Participants took part in two sessions of bisection task. In the single-range session (Session Single), the modality effect was facilitated by using the same anchor durations in both modalities (i.e., the 'experimental' condition), while in the double-range session (Session Double), susceptibility to the effect was reduced by using two different sets of anchor durations (i.e., the 'control' condition). In none of the sessions were participants informed whether the durations were the same for both modalities.

Method

Participants

Sixteen National University of Singapore students (aged 19-28, eight female) gave informed consent and took part in a two-session duration bisection experiment. Fifteen were right-handed according to the Edinburgh Handedness Inventory. They were naïve to the hypotheses of the experiment and were reimbursed for their participation.

Stimuli

Either an auditory or visual signal served as the carrier of the durations. The auditory tones were identical to those used in the previous experiments. The visual durations were carried by a black square (100 x 100 pixels) always presented at the center of the screen (1024 x 768 pixels) with a light grey background. Light grey was chosen to reduce fatigue due to bright contrasts.

Two sets of six logarithmically distributed probe durations, including the anchors, were used. They were 600 (S), 760, 945, 1184, 1480, 1852 (L) ms and 1060 (S), 1325, 1657, 2072, 2590, 3240 (L) ms, respectively. The S:L ratio was 1:3.06.

Procedures

The procedure was similar to Experiment 2 with the following exceptions. Participants completed two bisection task sessions separated by at least one week. In both sessions, durations carried by auditory and visual signals were intermixed in the same block. Every block began with presentation of the four anchors (auditory Short and Long, and visual Short and Long) in the training phase. Each anchor was presented three times in random order during this phase (cf. Penney et al., 2000). In the test phase, each probe duration was repeated 7 times (a total of 42 trials per probe). The presentation order was pseudo-randomized so that each probe was preceded by a nominally ‘short’ probe or ‘long’ probe with equal probability. Participants again

pressed a key with their index fingers to indicate their choice. To accommodate the need for more complex counterbalancing of experiment blocks (see below), response key assignment was not counterbalanced across participants. Participants always chose 'long' with the right index finger and 'short' with the left index finger. The maximum response time allowed was 3000 ms following probe offset.

The two sessions differed mainly in whether the same set of probe durations was used for each modality. The probe durations used are illustrated in Figure 5.1. In the Session Single Range (Session Single), the set of durations with 605 ms as the short anchor and 1852 ms as the long anchor was used for both modalities. In the Session Double Range (Session Double), different sets of durations were used for each modality. The Short anchor set was identical to that used in the Session Single. The Long anchor set referred to the durations with 1060 ms as the short anchor and 3240 ms as the long anchor. The combination of probe modality and duration set gave rise to two types of experimental block: Short-Visual-Long-Auditory (SvLa) and Long-Visual-Short-Auditory (LvSa). Different duration sets were used for each modality within a given block to maximize the chance that participants noticed the duration range difference between modalities and made independent bisection judgments with respect to the modality.

There were a total of six identical blocks (nine minutes each) in Session Single and eight blocks in Session Double (nine minutes each). Out of the eight blocks in Session Double, four consecutives identical blocks of SvLa or LvSa were presented first. Counterbalancing ensured that half of the participants finished SvLa then LvSa, and vice versa. As a result, there were fewer trials for each condition in Session Double (28 trials per condition) than in Session Single (42 trials). The order of Session Single and Double was also counterbalanced across participants, giving rise to the between-subject factor Sess.Order in subsequent analyses (see below).

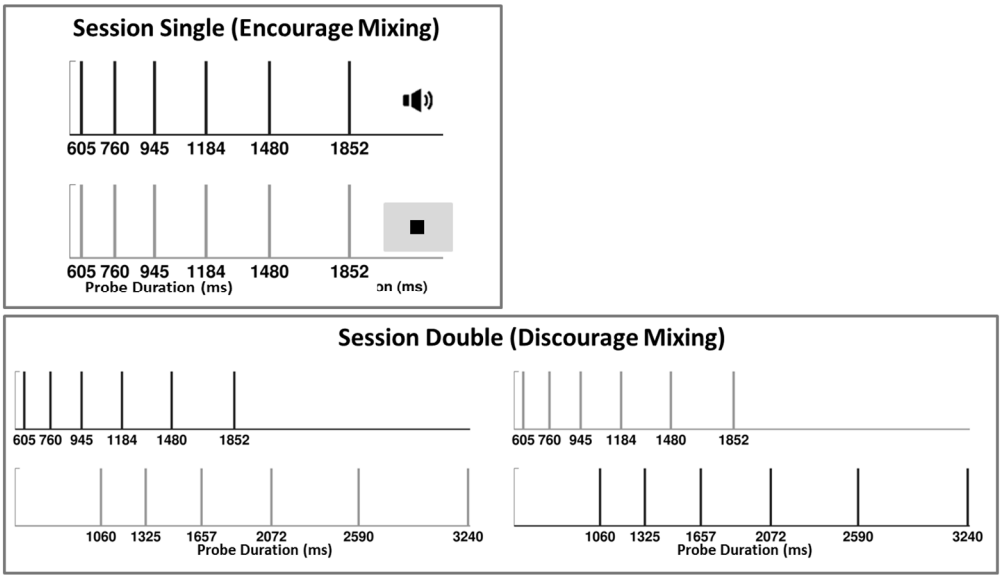


Figure 5.1. Probe durations used in Session Single and Double. The durations were the same for auditory (dark bars) and visual (grey bars) probes in Session Single to encourage mixing, while the durations were shorter for auditory than visual probes in half of the blocks (and vice versa) in Session Double.

The actual durations presented deviated slightly from the nominal durations, because of the involvement of visual signals, whose actual duration is limited by the refresh rate of the CRT monitor used in the experiment. To ensure any differences in bisection performance between modalities could not be due to timing variability of stimulus presentation, 1) visual durations were computed as integer multiples of the CRT refresh rate, 2) auditory durations were adjusted accordingly so that they either matched or were slightly longer than their visual counterparts, whichever matched better to the geometric spacing of the probe durations, and 3) stimulus presentation of both modalities were set to be synchronized with the screen refresh onset in E-prime. Stimuli were also adjusted so that they were neither too large nor too bright/dim for the participants, so that differences in subjective duration estimation due to stimulus magnitude should not be large enough to account for any effects (e.g., Xuan, Zhang, He, & Chen, 2007).

Results

Bisection Parameters

Subject estimates of PSE, DL, and WF were computed for each session by fitting the PLM to individual participant's psychometric functions. While we counterbalanced the session order across participants, so that half the participants finished Session Single then Session Double, Gamache and Grondin (2010) reported a session order effect in their bisection task examining the modality effect. To look at the possible carry-over effect on the modality difference in timing, we followed their approach and put session order (Sess.Order) into our analysis as well.

Table 5.1 summarizes the mean PSEs when Sess.Order was taken into account. One-sample *t*-tests (H0 = the PSE was not different from the GM) already indicated some differences between the subject group who finished Session Single in the first session and Session Double in the second (group Single-Double, SD) and the group who finished the experiment in the opposite order (group Double-Single, DS). For group SD, the auditory PSE in Session Single was shorter than the GM (by 95 ms, $p = .019$), the visual PSE in Session Double with Short anchor set was longer than the GM (by 186 ms, $p = .035$), and both PSEs in Session Double with Long anchor set were shorter than the GM (by 300 ms, $ps < .01$). In contrast, none of the PSEs in any condition was statistically different from the GMs in group DS.

Table 5.1

Summary of Mean PSEs and One-sample t-tests against the GM with Sess.Order taken into account

Point of Subjective Equality (PSE)						
Sess.Order	Condition	PSE (ms)	95% CI (ms)	GM (ms)	*t*	pvals
Single-Double (group SD)	Single V	1092	975-1209	1060	.75	.48
	Single A	961	888-1034		-3.039	.019*
	Double V short	1246	1073-1420		2.60	.035*
	Double A short	1049	987-1111		-.24	.82
	Double V long	1538	1379-1696	1852	-4.69	.0022**
	Double A long	1563	1426-1700		-5.00	.0016**
Double-Single (group DS)	Single V	1077	960-1194	1060	.44	.68
	Single A	1063	960-1167		.19	.86
	Double V short	1115	993-1237		1.16	.28
	Double A short	1119	993-1245		1.21	.27
	Double V long	1720	1525-1915	1852	-1.60	.15
	Double A long	1794	1593-1995		-.68	.52

Note: * indicates statistical significance at α = .05. ** indicates statistical significance at α = .0042

Figures 5.2 to 5.4 show the psychometric functions derived from grand average p('long')s. The PLM was fitted to each probe modality, anchor set, and session. For the Short anchor set (S = 605 ms, L = 1852 ms) in both Session Single (Figure 5.2) and Double (Figure 5.3), the visual response functions were right-shifted relative to the auditory response functions only in Group SD, but not Group DS. For the Long anchor set (S = 1060 ms, L = 3240 ms), there was no obvious difference in the central tendency between modalities. However, the PSEs of the Group SD was shifted to the left more than that those of Group DS (Figure 5.4).

Previous studies using a geometric probe series typically found the PSE to lie close to the GM (Allan & Gibbon, 1991) or below the AM (Kopec & Brody, 2010). It is argued that if the bisection criterion is predominantly influenced by the auditory durations (Penney et al., 2000), then the auditory PSE should lie close to the GM, while the visual PSE should lie far from either central tendency (Gamache & Grondin, 2010). However, for group SD in Session Single, the visual PSE in fact was numerically closer to the GM (1060 ms), while the auditory PSE was significantly

shorter than the GM (Figure 5.2). So for this group, it appears that visual durations contributed more to the common criterion.

Furthermore, the PSEs of the Long anchor sets in Session Double were both much shorter than the GM (1850 ms), again only for Group SD. This latter result suggests that 'memory mixing' also occurred in Session Double for these participants because the bisection criterion of the Long anchor set appeared to be affected by the durations from the Short anchor set (from the other modality) presented in the same block, such that it was pulled to a lower central tendency (Allan & Gerhardt, 2001).

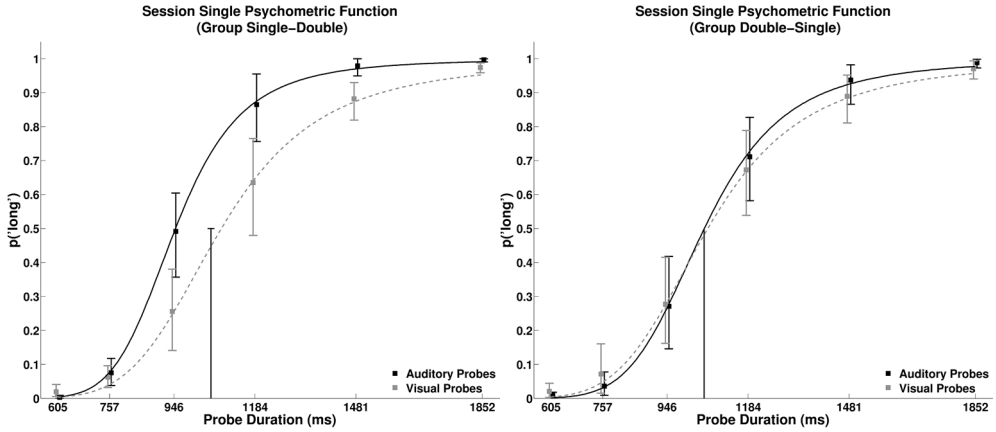


Figure 5.2. Group average psychometric functions for auditory (black square, black curve) and visual (grey square, dotted grey curve) probe durations in Session Single. Left: Psychometric functions from Group Single-Double. Right: Psychometric functions from Group Double-Single. The curves are PLM fits. Error bars are 95% bootstrapped CIs. The location of the GM (1055 ms) is marked with the black line extending to p('long') = .5.

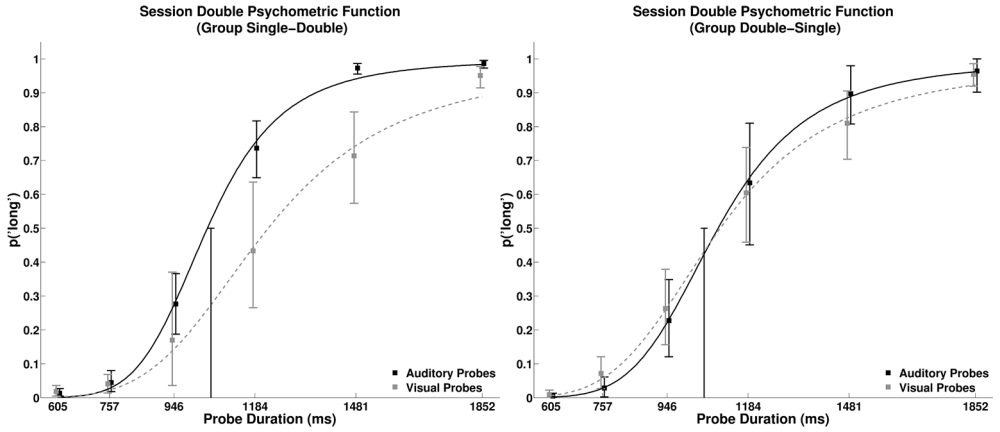


Figure 5.3. Group average psychometric functions for auditory (black square, black curve) and visual (grey square, dotted grey curve) probe durations in Session Double, Short anchor condition (S = 605, L = 1852 ms). Left: Psychometric functions from Group Single-Double. Right: Psychometric functions from Group Double-Single. The curves are PLM fits. Error bars are 95% bootstrapped CIs. The location of the GM (1055 ms) is marked with the black line extending to p('long') = .5.

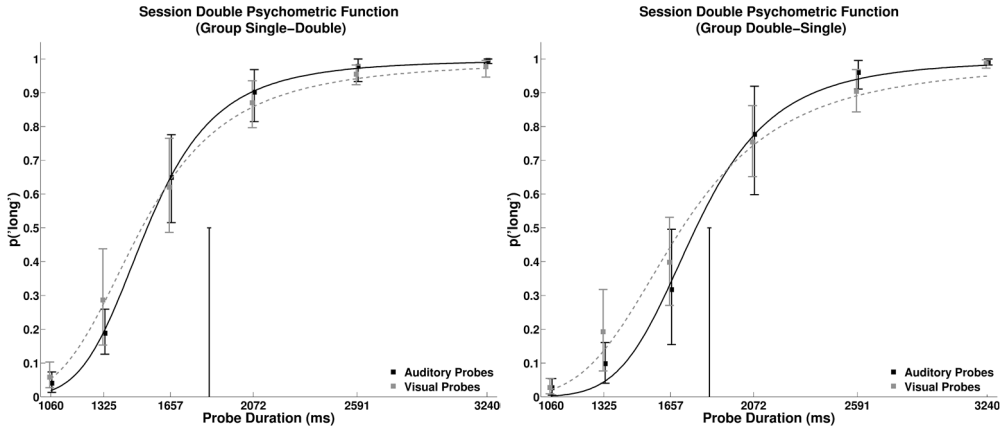


Figure 5.4. Group average psychometric functions for auditory (black square, black curve) and visual (grey square, dotted grey curve) probe durations in Session Double, Long anchor condition (S = 1060, L = 3240 ms). Left: Psychometric functions from Group Single-Double. Right: Psychometric functions from Group Double-Single. The curves are PLM fits. Error bars are 95% bootstrapped CIs. The location of the GM (1852 ms) is marked with the black line extending to p('long') = .5.

Despite the presence of memory mixing in Session Double (in half of the participants), the PSEs of the Long anchor set were still differentiable from the PSEs of the Short anchor set, as indicated by the non-overlapping confidence intervals (Table 5.1 and Figure 5.5). This suggests that participants were aware that different duration sets were used and tried to respond accordingly (Klapproth, 2009; Spínola et al., 2013; Wearden et al., 2006).

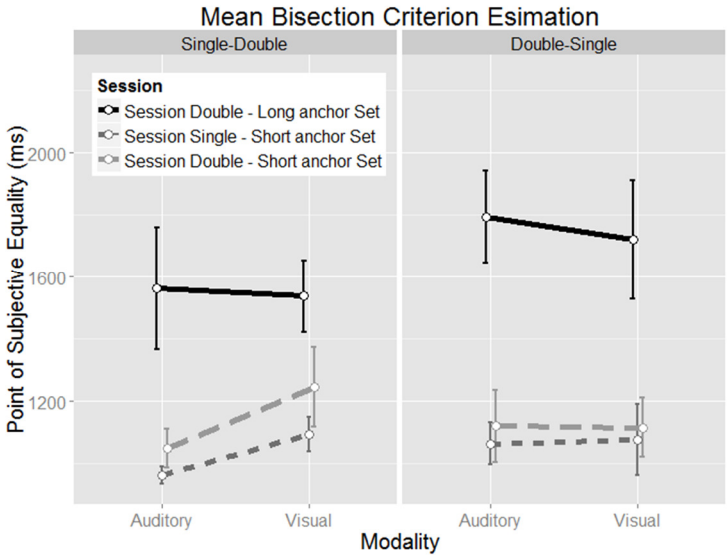


Figure 5.5. Mean PSEs according to Sess.Order (left = group SD and right = group DS), Modality, and the absolute durations of S and L (dark grey = 605/1852 ms in Session Single, light grey = 605/1852 ms in Session Double, black = 1060/3245 ms in Session Double). Error bars represent within-subject 95% CIs.

Pairwise results based on *t*-tests of the PSEs were complemented by ANOVAs to look at the changes in PSE across sessions and groups. For the purpose of the current study, data from Session Single and the Short anchor set in Session Double (both used the same S and L, 605 and 1852 ms, respectively) were subject to one ANOVA, with the latter serving as the 'control' of the former (i.e., the four 'lower' points in each of the panels in Figure 5.5), and the data from the Long anchor set in Session Double (S = 1060 ms, L = 3240 ms) were subject to a separate ANOVA.

For the data from the Short anchor sets, a Three-way mixed ANOVA with Sess.Order as the between-subjects factor and Session and Modality as the within-subjects factors revealed a significant Sess.Order x Modality interaction, $F(1,14) = 10.52$, $p = .006$, ges = .086 (Figure 5.6, left). The interaction was further examined by collapsing the data across sessions (Figure 5.6, right). The within-subjects 95% CIs suggested a modality effect was present in group SD, $F(1,7) = 13.95$, $p < .001$, ges = .31, but not group DS, $F(1,7) = .044$, *n.s.*, consistent with the impression from the one-sample *t*-test results. In Group SD, the direction of the difference in PSEs was

consistent with the memory mixing effect (Penney et al., 2000; Wearden et al., 1998). Within each modality, the between Sess.Order comparison was not significant.

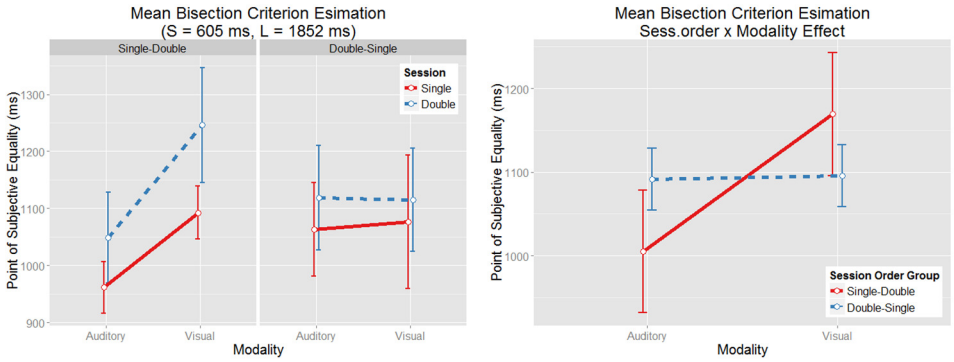


Figure 5.6. Left: Mean PSEs of experimental blocks using the Short duration series (S = 605 ms, L = 1852 ms) according to Modality, Session (solid = Session Single, dotted = Session Double), and Sess.Order (left = group SD, right = group DS). Right: Mean PSEs depicted in the Sess.Order x Modality interaction. Error bars represent within-subject 95% CI.

There was also a main effect of Session, $F(1,14) = 8.76$, $p = .0010$, ges = .094, suggesting that the PSEs were generally longer in Session Double. As discussed above, this was likely to be due to the memory mixing with the durations from the longer anchors (S = 1060 ms, L = 3240 ms; Gu & Meck, 2011). All in all, using probe modality and changes in duration range, we created differences in PSE between sessions and a group-specific 'sound longer than light' effect.

Finally, for the data from the Long anchor set, a Two-way mixed ANOVA with Sess.Order and Modality as factors yielded a significant main effect of Sess.Order, $F(1,14) = 9.47$, $p = .008$, ges = .22, consistent with the one-sample *t*-test results that the PSE from Group SD was shorter than the GM, but the PSE from Group DS was not (Figure 5.5, top black lines).

For the DL, Figure 5.7 suggests a similar pattern of temporal sensitivity between Sess.Order groups. A Three-way mixed ANOVA revealed a significant main effect of Modality, $F(1,14) = 13.67$, $p = .0024$, ges = .15, implying that Sess.Order did not affect temporal sensitivity. Also, the higher temporal sensitivity in auditory perception is replicated (e.g., Welch, DuttonHurt, & Warren, 1986).

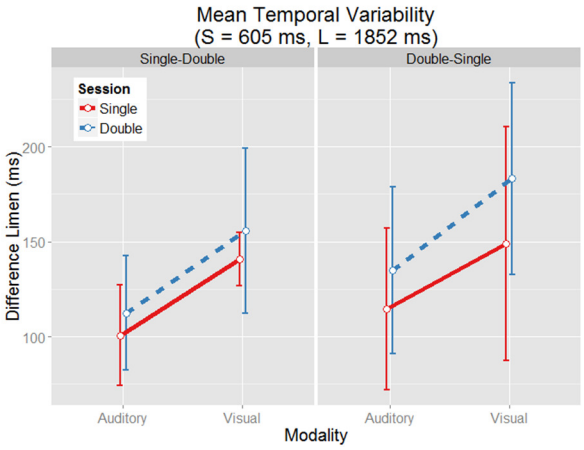


Figure 5.7. Mean Difference Limens (DL) of Session Single (solid) and Session Double (dotted) for group SD (left) and group DS (right). Error bars represent within-subject 95% CI.

For the WF, Figure 5.8 suggests qualitatively similar patterns of sensitivity between Sess.Order groups. A Three-way mixed ANOVA again revealed only a significant main effect of Modality, $F(1,14) = 9.64$, $p = .0078$, ges = .12, replicating the better temporal sensitivity in auditory stimuli, even when both types of stimuli were intermixed. Graphically, the same can be concluded from the flatter visual psychometric functions (Figures 5.2-5.4). The values of the WF were within the range of .1 to .15, indicating good bisection discrimination.

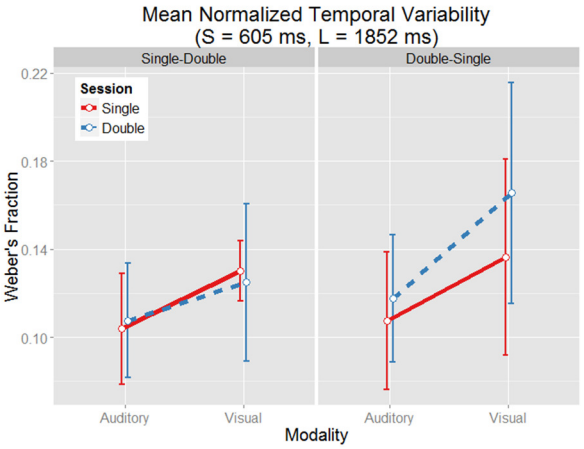


Figure 5.8. Mean Weber Fractions (WF) of Session Single (solid) and Session Double (dotted) for group SD (left) and group DS (right). Error bars represent within-subject 95% CI.

Ex-Gaussian RTs

Since our major interest is in the modality effect, our analysis of RTs is focused on this session. The Three-way mixed ANOVA (Sess.Order, Modality, and Probe Duration) on ex-Gaussian *Mu* (Figure 5.9) yielded significant main effects of

Modality, $F(1,14) = 15.47$, $p < .001$, ges = .21, and Probe Duration, $F(5,70) = 5.42$, $p = .035$, ges = .018, suggesting that visual *Mu* was longer than auditory *Mu*. For the main effect of Probe Duration, contrasts against Probe 3 as baseline (Table 5.2) showed that the significant decrease in *Mu* occurred at Probe 5 (1480 ms; Figure 5.10).

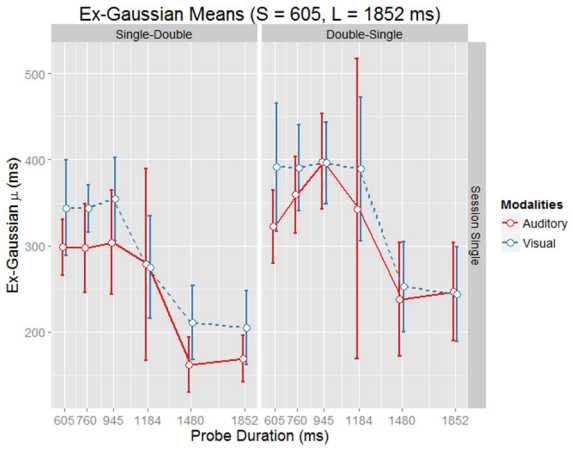


Figure 5.9. Estimated mean ex-Gaussian *Mu* of each probe duration as a function of Modality (solid = auditory, dotted = visual) and Sess.Order group (left = SD, right = DS) in Session Single. Error bars represent within-subject 95% CIs.

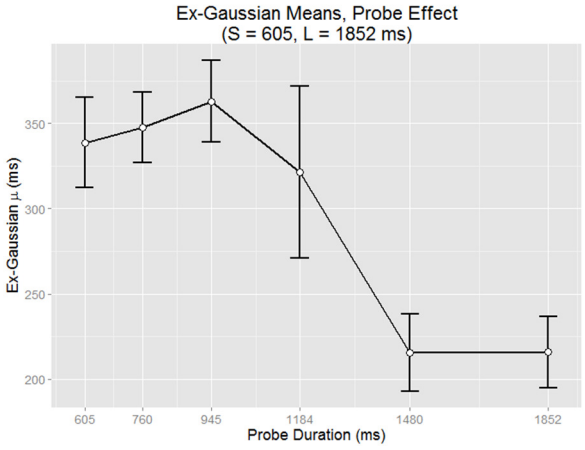


Figure 5.10. Estimated mean *Mu* of each probe duration collapsed over Modality in Session Single. Error bars represent within-subject 95% CIs.

Table 5.2

Summary of Contrasts on the Probe Duration Effect for Mu in Session Single

	coef	t	p val
Probe 3 vs. Probe 1	-24.24	-1.35	.20
Probe 3 vs. Probe 2	-15.51	-1.18	.26
Probe 3 vs. Probe 4	-41.70	-1.51	.15
Probe 3 vs. Probe 5	-147.53	-6.85	.0000050*
Probe 3 vs. Probe 6	-146.99	-7.16	.0000031*

Note: * indicates statistical significance at α = .05.

Figure 5.11 shows the ex-Gaussian *Sigma*. The mixed ANOVA yielded a main effect of Probe Duration, $F(5,70) = 8.82$, $p = .0025$, ges = .18 (Figure 5.12). Contrasts against Probe 3 (945 ms) as baseline showed that RT variability at Probe 3 was larger than all probe durations except Probe 4, the probe with duration next nearest to the GM (Table 5.3). The 95% CIs in Figure 5.12 also suggest that *Sigma*-s were smaller for the two longest probe durations.

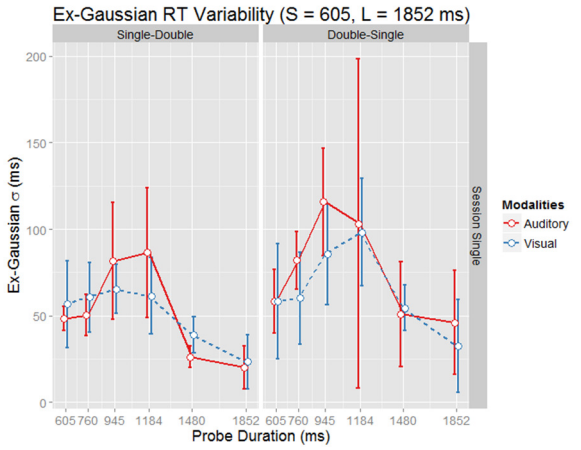


Figure 5.11. Estimated mean ex-Gaussian *Sigma* of each probe duration as a function of Modality (solid = auditory, dotted = visual) and Sess.Order group (left = SD, right = DS) in Session Single. Error bars represent within-subjects 95% CIs.

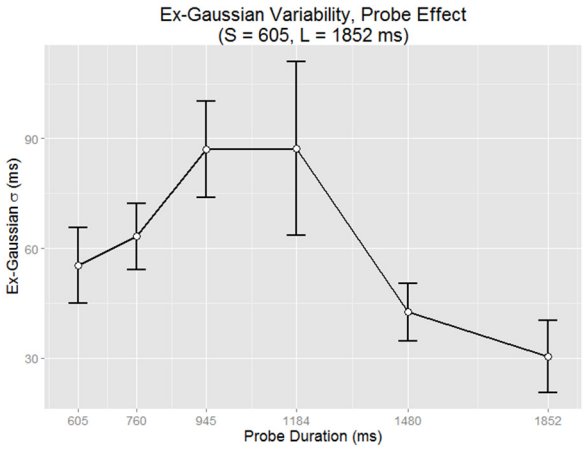


Figure 5.12. Mean *Sigma* of each probe duration depicted in the Probe Duration main effect. Error bars represent within-subjects 95% CIs.

Table 5.3

Summary of Contrasts on the Probe Duration Effect for Sigma in Session Single

	coef	t	p val
Probe 3 vs. Probe 1	-31.76	-4.045	.0011
Probe 3 vs. Probe 2	-23.856	-3.44	.0036
Probe 3 vs. Probe 4	.24	.016	.99
Probe 3 vs. Probe 5	-44.56	-7.49	.0000019*
Probe 3 vs. Probe 6	-56.64	-8.13	.00000070*

Note: * indicates statistical significance at α = .05.

Figure 5.13 shows the ex-Gaussian *Tau*. The Three-way mixed ANOVA yielded significant Modality x Probe Duration interactions, $F(5,70) = 3.06$, $p = .046$, ges = .011. The interaction effect was further examined in each Modality with contrasts against Probe 3 as the baseline (Table 5.4). For auditory probes, *Tau*-s at Probe 3 was longer than all except Probe 4, while for visual probes, *Tau*-s at Probe 3, were longer than all except Probe 4 and 5 (Figure 5.14). Therefore, the extreme RTs were shifted to longer probe durations in the visual domain.

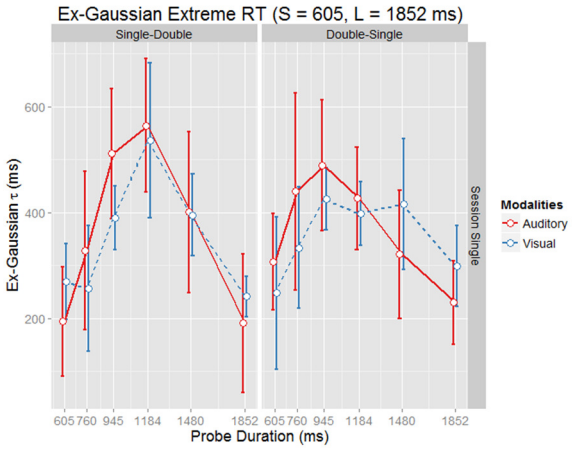


Figure 5.13. Estimated mean ex-Gaussian *Tau* of each probe duration as a function of Modality (solid = auditory, dotted = visual) and Sess.Order group (left = SD, right = DS) in Session Single. Error bars represent within-subject 95% CI.

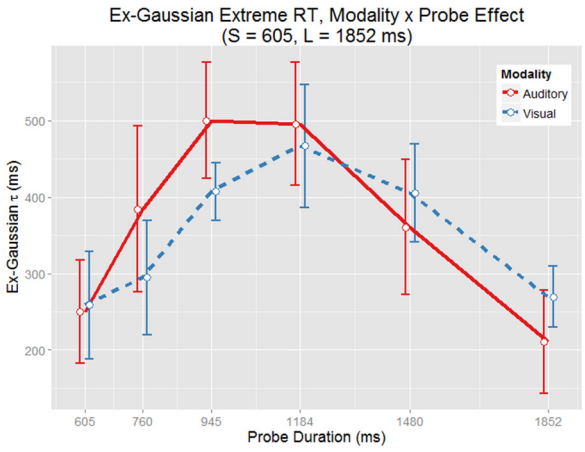


Figure 5.14. Mean *Tau* of each Probe Duration (solid = auditory, dotted = visual) by Modality in Session Single. Error bars represent within-subject 95% CIs.

Table 5.4

Summary of Contrasts on the Probe Duration Effect for Tau in Session Single

	Auditory			Visual		
	coef	t	p val	coef	t	p val
Probe 3 vs. Probe 1	-249.74	-4.99	.00016*	-148.49	-3.92	.0014*
Probe 3 vs. Probe 2	-116.08	-2.60	.020*	-112.40	-3.65	.0024*
Probe 3 vs. Probe 4	-4.52	-0.12	.90	59.56	1.49	.16
Probe 3 vs. Probe 5	-139.36	-2.24	.041*	-1.76	-.049	.96
Probe 3 vs. Probe 6	-289.66	-5.00	.00016*	-137.56	-5.47	.000065*

Note: * indicates statistical significance at $\alpha = .05$.

Therefore, there was no Sess.Order effect in the analysis of RT. Similar to the previous experiments, there was a sudden drop in RT once the duration exceeded the GM. Variability and extreme responses were the largest for probes nearest to the GM, suggesting the difficulty in differentiating the probe durations from the bisection criterion. Interesting, there was a modality effect in both *Mu* and *Tau*. The auditory *Mu* was shorter than visual *Mu*, while the distribution of *Tau* was shifted to the left in auditory probes relative to the visual probe durations.

Changes in the CNV Time Course

Mean amplitudes. The grand average ERPs of each probe duration for each modality and session (S = 605 ms, L = 1852 ms) are shown in Figures 5.15 and 5.16. We first verified the general changes in the CNV by an amplitude analysis. Epochs from the two longest probes (1480 ms and 1852 ms) were used to generate the subject average ERPs (Figure 5.17). Mean amplitudes of 200 ms time windows, centered at each of the first five probe durations, were constructed. A Four-way mixed ANOVA revealed a significant Sess.Order x Session x Time Window interaction, $F(5,70) = 4.31$, $p = .0075$, ges = .026, and a significant Session x Modality interaction, $F(1,14) = 6.12$, $p = .027$, ges = .017.

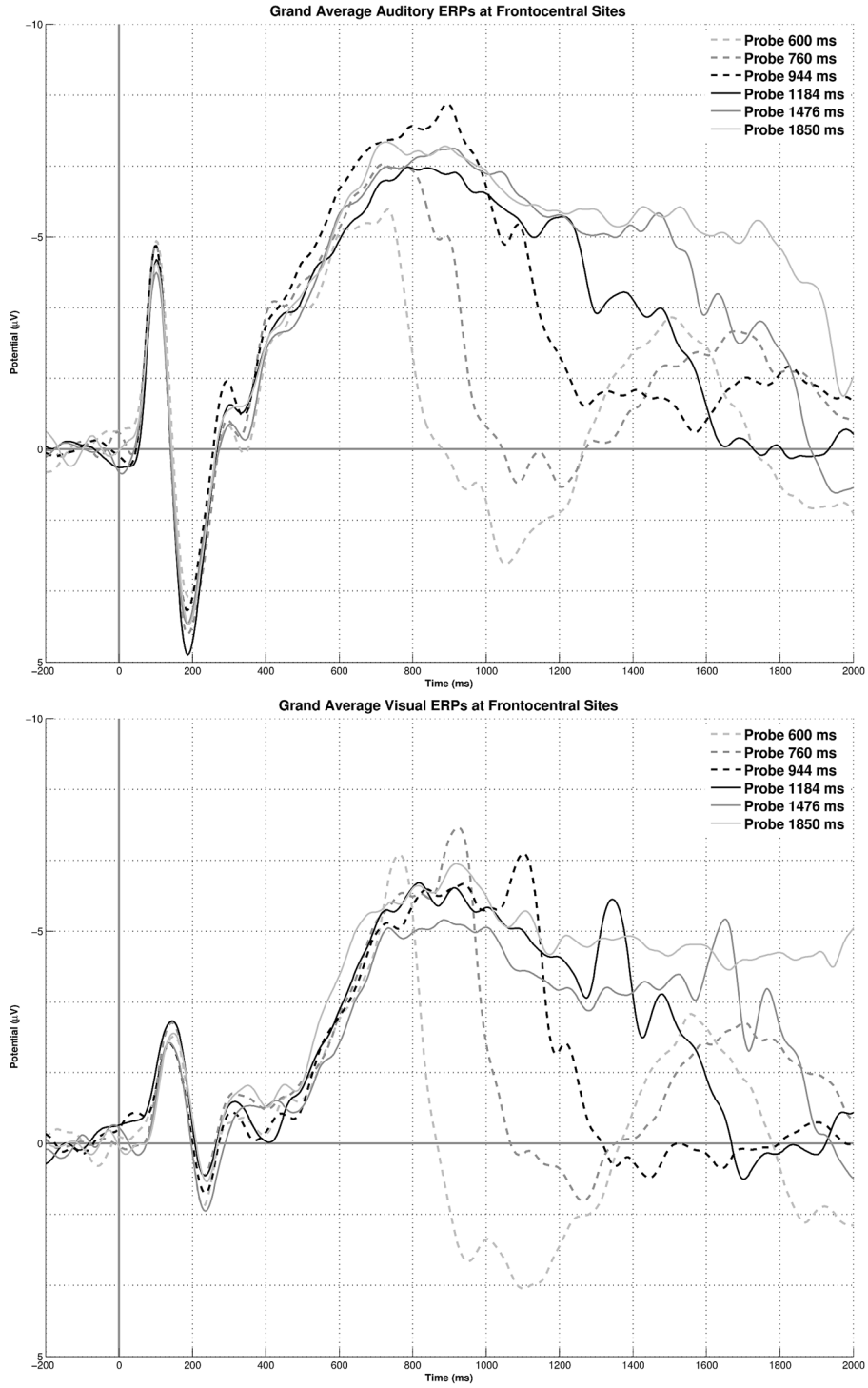


Figure 5.15. Grand average ERPs at fronto-central sites for auditory probes (top) and visual probes (bottom) from Session Single Range.

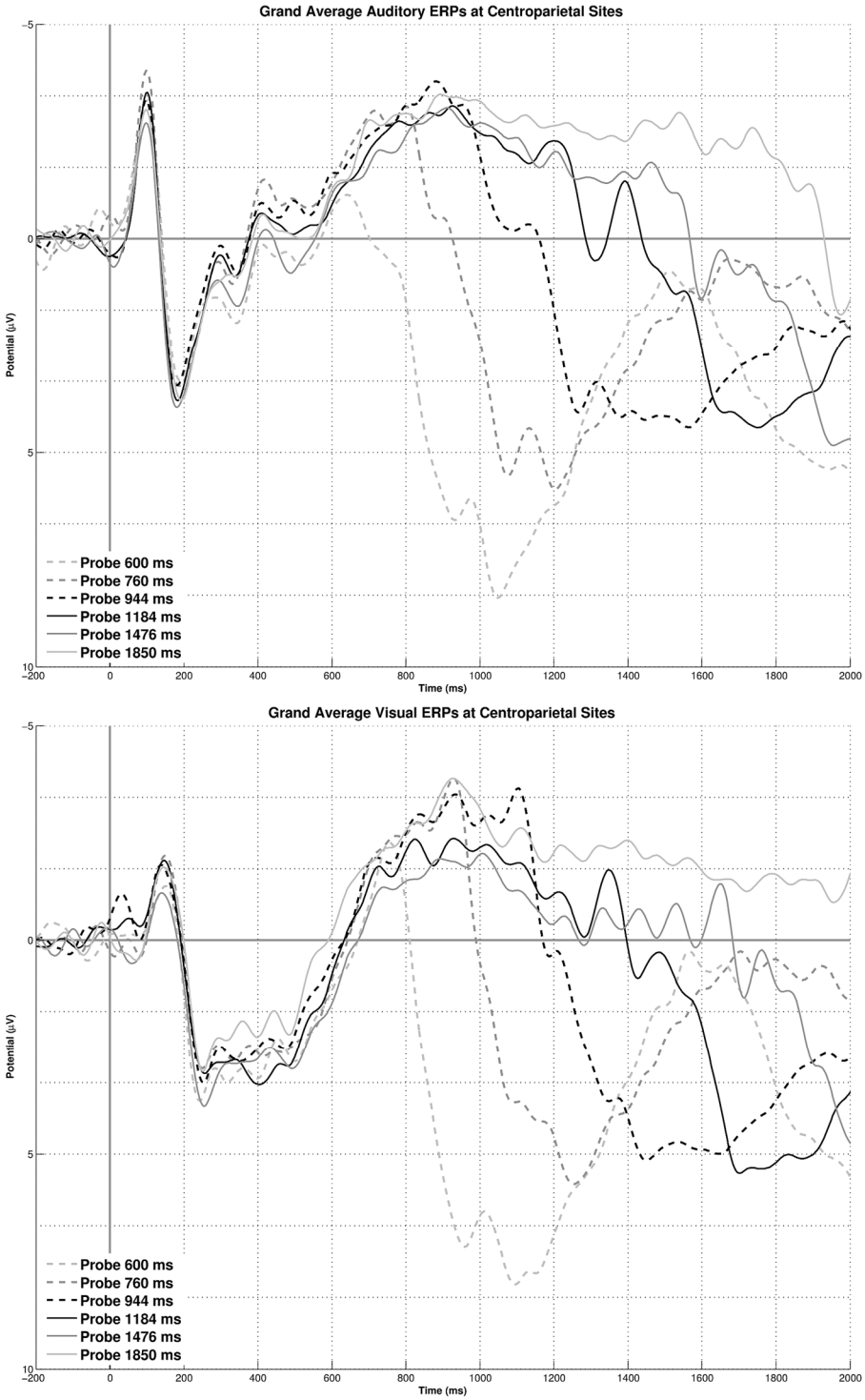


Figure 5.16. Grand average ERPs at centro-parietal electrodes for auditory probes (top) and visual probes (bottom) from Session Single Range.

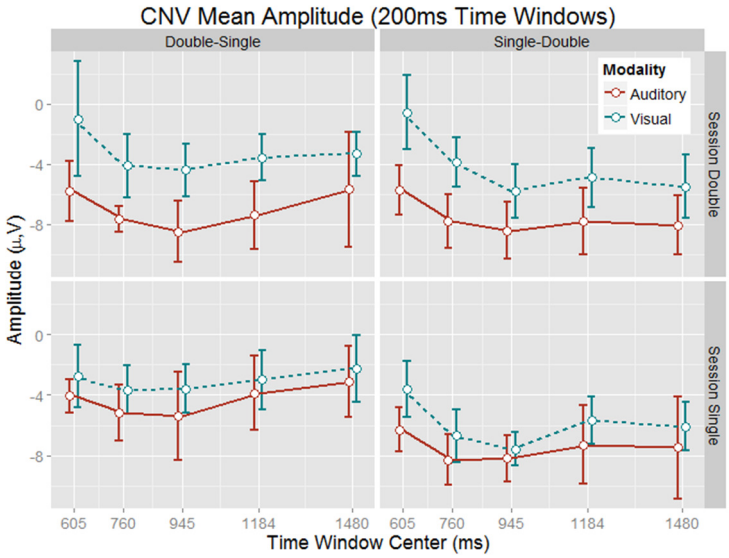


Figure 5.17. Mean CNV amplitude as a function of Modality (solid = auditory, dotted = visual), Session Order group (right column = group SD, left column = group DS), Session (lower row = Session Single, upper row = Session Double), and Time Window. Error bars represent between-subject 95% CIs.

The Three-way interaction was further examined in each session. In Session Single, there was a main effect of Sess.Order, $F(1,14) = 7.64$, $p = .015$, ges = .29, and Time Window, $F(5,70) = 11.63$, $p < .001$, ges = .17. The Sess.Order effect suggests that the CNV in general was more negative in Group SD (Figure 5.18, right panel). In Session Double, there was a main effect of Time window, $F(5,70) = 7.03$, $p = .0038$, ges = .21. The Time Window effects in each session were further explored by using contrasts against Probe 3 (945 ms) as baseline (Table 5.5). In Session Single, the CNV amplitudes were significantly less negative at Time Window 1, 4, and 5, suggesting peaking of amplitude near the GM. In Session Double, the CNV amplitudes were significantly less negative at all except the last time window, again suggesting peaking near GM.

For the Modality x Session interaction, the modality difference was not significant in Session Single, $t(25.69) = -.96$, $p = .35$, but it was in Session Double, $t(29.31) = -3.64$, $p = .0010$, showing a more negative auditory CNV than visual CNV in Session Double.

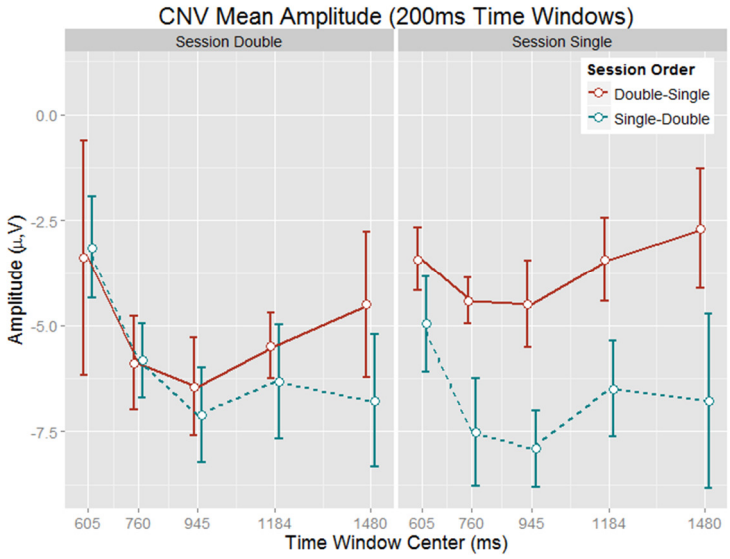


Figure 5.18. Mean CNV amplitudes depicted in the Sess.Order x Session x Time Window interaction. Error bars represent within-subject 95% CIs.

Table 5.5

Summary of CNV Mean Amplitude Contrasts with the Probe = 945 ms as Baseline

CNV-200ms	Session Single			Session Double		
	coef	t	p val	coef	t	p val
Probe 3 vs. Probe 1	2.00	4.55	.00039*	3.50	4.78	.00024*
Probe 3 vs. Probe 2	.23	1.031	.32	.92	2.72	.016*
Probe 3 vs. Probe 4	1.23	4.26	.00069*	.87	2.99	.0091*
Probe 3 vs. Probe 5	1.46	2.88	.011*	1.15	1.68	.11

Note. * indicates significance at α = .05.

PLSC analyses on modality and session effects. Based on the two PSE effects, we further proceeded to examine the CNV changes by 1) looking at the session effect (i.e., $PSE_{Single} < PSE_{Double}$) across the whole sample (N =16) and 2) looking at the modality effect in group SD and DS (cf. Keil, Mussweiler, & Epstude, 2006). For these analyses, the ERPs were obtained by averaging epochs from the two longest probes receiving a Long response according to condition.

For the session effect, PLSC analyses were conducted separately for auditory and visual probe durations. For auditory probes, the LV was not significant, $p = .086$. With a threshold bootstrap ratio = 2.57, stable salience was reported at frontal and fronto-central electrodes between 800 and 1200 ms, with the CNV in Session Double being more negative than in Session Single (Figure 5.19). For visual probes, the LV

was significant, $p = .002$. With a threshold bootstrap ratio = 2.57, stable salience was reported at central electrodes between 410 and 746 ms, and at parietal and occipital electrodes from 410 to the end of epoch (1480 ms) with the CNV in Session Double being more negative than in Session Single (Figure 5.20).

For the modality effect, PLSC analyses (df = 2) were conducted separately on each session, in which ERPs of each Modality and Sess.Order group were included. In Session Single, the first latent variable was significant, $p = .014$, and explained 87.77% of the covariance. However, the LV only captured the differences in evoked potentials between modalities. The salience (bootstrap ratio = 2.57) indicated very limited differences at the CNV time window (Figure 5.21 left). The brain scores (Figure 5.22 left) further indicated the marked between-modality differences in the ERPs. In Session Double, the first latent variable was significant, $p < .001$, and explained 92.81% of the covariance. The LV captured the differences in evoked potentials between modalities as well as the CNV differences. The salience (bootstrap ratio = 2.57) indicated differences between 400 – 900 ms (Figure 5.21 right). The brain scores (Figure 5.22 right) further indicated the between-modality differences in the ERPs. More important, although the PSE analyses indicated that only group SD expressed the modality effect (significant Modality x Sess.Order interaction), the differences in the ERPs were qualitatively similar across both groups, regardless of the occurrence of the modality effect. When there was a difference, the pattern was not consistent: The brain scores showed that when it was Session Single, the difference between visual and auditory ERPs was larger in group SD than group DS; however, this was reversed in Session Double.

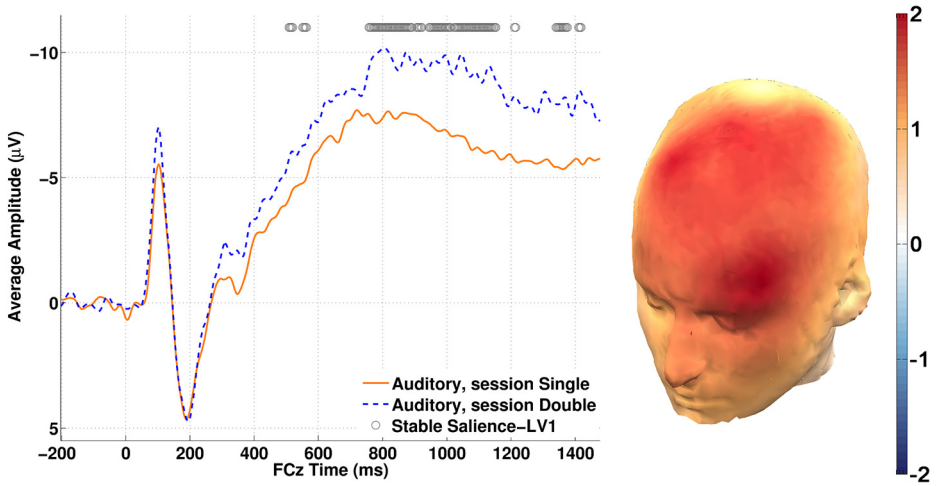


Figure 5.19. Left: Representative grand average ERPs of auditory probes from Session Single (solid) and Double (dotted) at FCz. Stable salience (bootstrap ratio > 2.57; although the LV was not significant) is marked by dark circles at the top of the panel. Right: topographical distribution of the electrode salience between 410 and 746 ms.

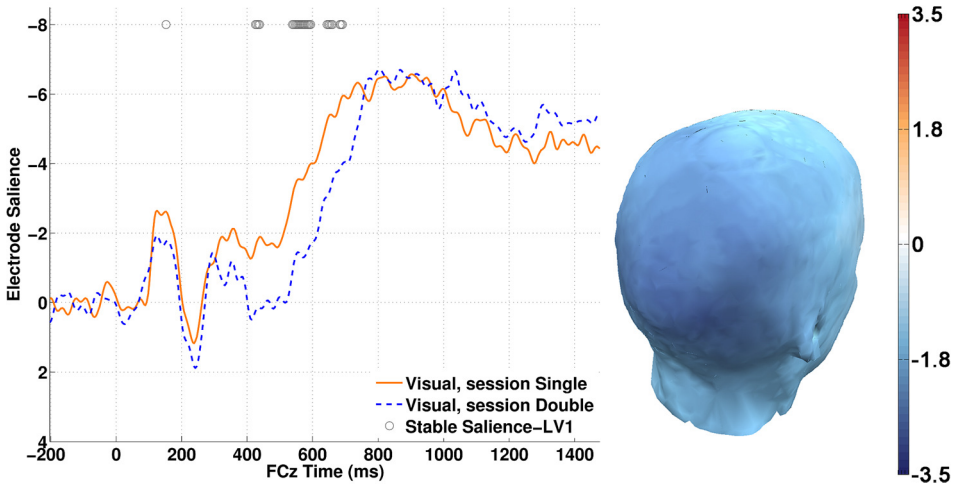


Figure 5.20. Left: Grand average ERPs of visual probes from Session Single (solid) and Double (dotted) at FCz. Stable salience (bootstrap ratio > 2.57) is marked by circles at the top of the panel. Right: topographical distribution of the electrode salience between 400 and 900 ms.

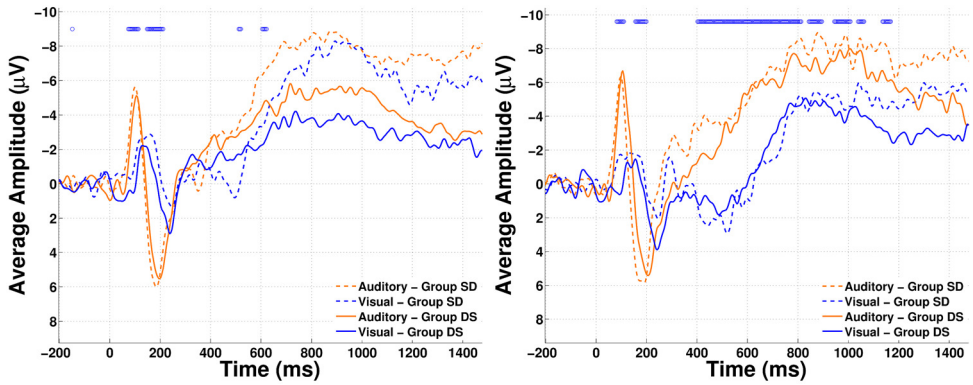


Figure 5.21. Left: Grand average ERPs of auditory (orange) and visual (blue) probes from the two Session Order groups (group SD = dotted, group DS = solid) during Session Single at electrode Cz. Right: Same ERPs from Session Double. In each panel, stable salience (bootstrap ratio > 2.57) is marked by circles at the top of the panel.

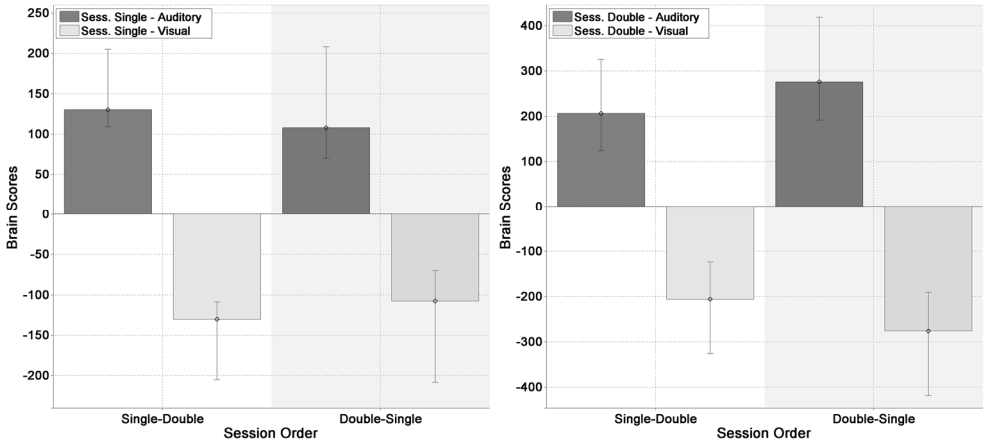


Figure 5.22. Brain scores obtained in Session Single (left) and Double (right). Brain scores of auditory probes (dark grey bars) and visual probes (light grey bars) from group SD are presented in the white area of each panel, while those from group DS are presented in the shadowed area of each panel. Error bars represent bootstrap 95% CIs.

Slope changes on modality and session effects. The results from Experiment 2 suggest it is possible that the CNV resolves before or at the criterion time. The differences in PSE observed here imply that the bisection criterion was reached earlier for auditory probes than visual probes, and it was reached earlier in Session Single than Session Double. If the CNV resolution reflects the end of the bisection criterion, then differences in the CNV resolution latency between conditions should obtain, even if timing is not exact. To this end, mean CNV amplitudes and slopes were obtained for auditory and visual ERPs separately. Figure 5.23 shows the grand average ERPs for each Session, Modality and Session Order group.

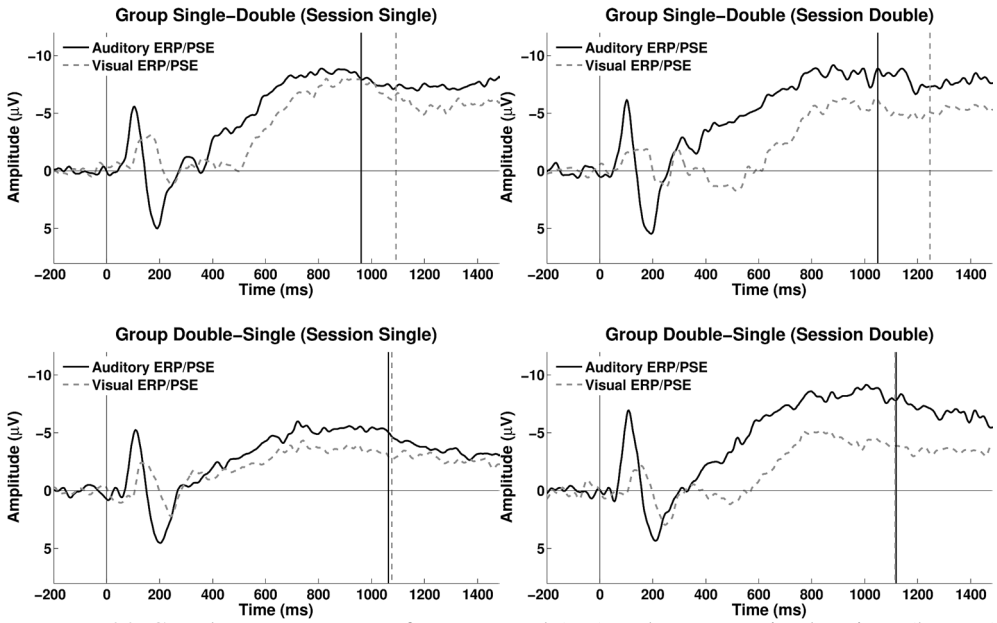


Figure 5.23. Grand average ERPs at fronto-central (top) and centro-parietal regions (bottom) from Session Single. In each figure, solid curves depict the smoothed auditory ERPs, dotted curves depict the smoothed visual ERPs. Vertical dotted lines mark the PSEs of auditory probe durations (1012 ms) and visual probe durations (1084 ms), collapsed across Sess.Order groups. Each ERP is an averaged signal of six fronto-central or centro-parietal electrodes.

For the Session effect (i.e., $PSE_{Single} < PSE_{Double}$), the time windows for auditory probes were defined according to the difference between group fit PSE (Table 5.6), i.e. 1084-1012 = 72 ms, such that mean CNV amplitudes and slopes were computed at 940-1012, 1012-1084, and 1084-1156 ms. The CNV was expected to resolve at different time windows if resolution happens close to the end of the respective bisection criterion. Therefore, the interaction between Time Window and Session was expected to be statistically significant. However, this was not the case when Three-way mixed ANOVAs (Sess.Order x Session x Time Window) were conducted, $F(2,30) = .40$ for CNV amplitude and $F(2,30) = .14$, for CNV slope (Figure 5.24 solid lines).

The time windows for visual probes were defined as 1181-1084 = 97 ms, such that mean CNV amplitudes and slopes were computed at 987-1084, 1084-1181, and 1181-1278 ms. Again, none of the interactions were significant, $F(2,30) = .017$ for amplitude and $F(2,30) = 2.16$, $p = .13$ for slope (Figure 5.24, dotted lines).

For the session-order-moderated modality effect (present only in participants from group Single-Double, group SD; Table 5.1), the analyses proceeded in a similar fashion, except that the data was only from Session Single, i.e. the replacement of the within-subjects factor Session with the between-subjects factor Sess.Order. We expected to obtain interactions involving Sess.Order and Time Window if changes in CNV amplitude and/or slope reflected the differences in reaching the bisection criterion in the two Session Order groups (Figure 5.25). For amplitude, a Three-way mixed ANOVA (Sess.Order x Modality x Time Window) did not yield any significant interaction effects. For slope, the ANOVA yielded only a Sess.Order x Modality interaction, $F(1,14) = 10.00$, $p = .0069$, ges = .023. Paired sample t tests within each Session Order group showed that the visual slope was more positive than auditory slope in group SD, $t(7) = 3.17$, $p = .016$, while there was no significant difference between the two CNV slopes in group DS, $t(7) = 1.30$, $p = .24$ (Figure 5.26).

Table 5.6.

Summary of Mean PSEs (N = 16) and One-sample t-tests Results against GMs

Point of Subjective Equality (PSE)				
Condition	PSE (ms)	GM (ms)	*t*	p val
Single V	1084	1060	0.84	.41
Single A	1012		-1.43	.171
Double V short	1181		2.61	.020*
Double A short	1084		0.93	.37
Double V long	1629	1852	-3.82	.0017*
Double A long	1678		-2.90	.011*

Note: * indicates significance at α = .05.

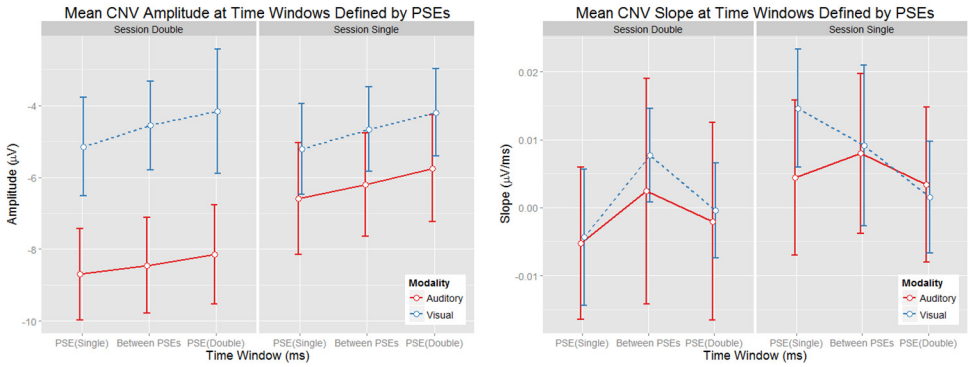


Figure 5.24. Mean CNV amplitudes (left panel) and slopes (right panel) of auditory (solid lines) and visual (dotted lines) probes at specific time windows (until PSE(Single), between PSE(Single) and PSE(Double), and after PSE(Double)) for the Session effect (Session Single < Double) on PSE. Error bars represent within-subject 95% CIs.

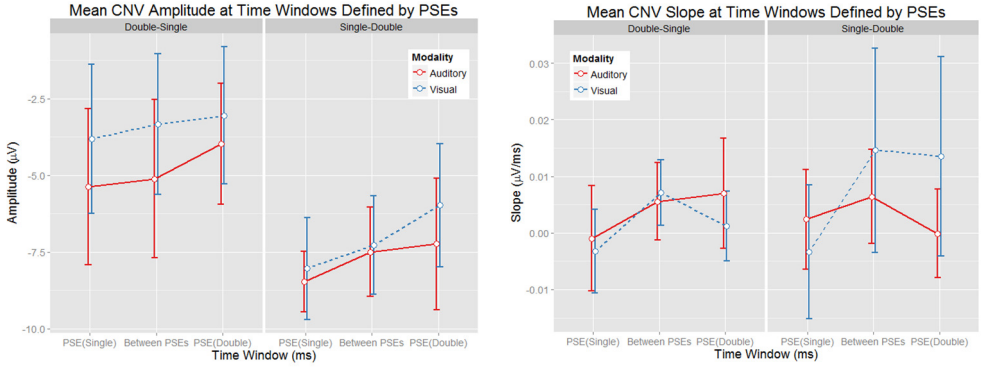


Figure 5.25. Mean CNV amplitudes (left panel) and slopes (right panel) of auditory (solid lines) and visual (dotted lines) probes at specific time windows (until PSE(Single), between PSE(Single) and PSE(Double), and after PSE(Double)) for the Modality effect (present in group Single-Double only) on PSE. Error bars represent within-subject 95% CIs.

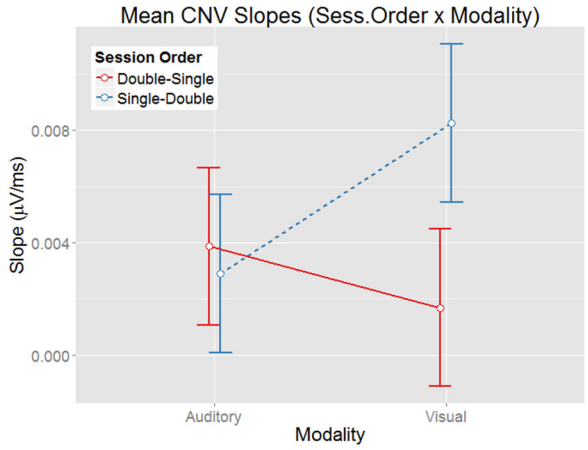


Figure 5.26. Mean CNV slopes for Session Order by Modality. Error bars represent within-subject 95% CIs.

Principal Component Analysis

Finally, the data from the two longest probe durations of each modality were subject to PCA as in Experiment 2. Again, the data were first CSD transformed to reduce volume conduction. The first PC was a bilateral negativity, explaining 57.4% of the covariance and having a sustained time course. To examine this PC in greater detail, the factor scores at FC3/FC5, C3/C5, FC4/FC6, and C4/C6 were averaged into two regions of interest (ROI) on each hemisphere, similar to Experiment 2. A Two-way repeated measures ANOVA with Modality and ROI as within-subject factors yielded significant main effects of Modality, $F(1,15) = 10.86$, $p = .0049$, ges = 11, and ROI, $F(1,15) = 8.29$, $p = .011$, ges = .13. These effects suggest that PC1 was more negative in auditory probes in general and on the right hemisphere regardless of modality (Figure 5.27). This topographical distribution is consistent with Coull et al.'s (2004) fMRI study showing the role of the right inferior frontal gyrus as temporal attention. Finally, PC2 showed the typical fronto-central distribution of the CNV, however the time course suggests that it peaked early (before 600 ms) and did not match the sustained negativity (Figure 5.27).

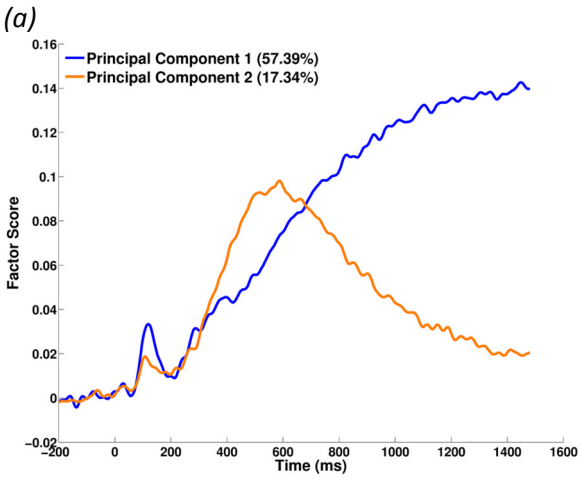


Figure 5.27. (a) Time courses of the first two principle components (PCs). (b) Left: Mean factor scores on the left and right regions of interest (FC3/FC5 and C3/C5 vs. FC4/FC6 and C4/C6). Right: Topographical distributions of the factor scores captured in PC1.

Discussion

In this experiment, we used the modality effect on time perception to introduce discrepancies in the bisection criterion between conditions (Penney et al., 2000; Wearden et al., 1998). This modality effect was replicated in half of the participants. In addition, there was a session effect: given the same S and L, the PSE in Session Double was longer than that in Session Single. Nevertheless, we did not find any systematic changes in the CNV that fit with the pacemaker-accumulator interpretation of the CNV. PCA showed that the sustained negativity was again bilaterally distributed regardless of modality, being stronger when probes were auditory and on the right hemisphere.

Psychometric Parameters

Using durations between .5 and 2 seconds, we reproduced the observation that sounds are judged longer than lights (e.g., Goldstone & Lhamon, 1974), as shown by the shorter PSE for auditory probes in Session Single, in which anchor and probe durations from both modalities were presented in the same experimental blocks. Interestingly, a shortened auditory PSE was also observed in Session Double with short anchor durations, a condition that was aimed to serve as a control. Overall the modality effect size was not large, and the effect was moderated by the order of the experimental sessions. Finally, as expected, the temporal sensitivity to auditory probes was higher, replicating previous findings.

An instructional interpretation may explain the session order effect. For participants in group DS, they first completed the session during which different anchor durations were used for each modality. They would have become aware that comparisons should be made with respect to the anchors or criterion of the same modality, despite ambiguity in the instructions. This knowledge was likely to be carried over to the second session; despite the ambiguous instructions and actual identity of the anchor durations used in Session Single, they continued to use the same strategy and made comparisons only within modality, resulting in the absence of a modality effect. This relation between task knowledge and timing performance receives support from other studies. For instance, Tobin and Grondin (2012) examined the accuracy of temporal estimation and production in a group of elite swimmers. Their results showed that the swimmers timed better when they could better apply their knowledge about swimming to the timing tasks (e.g., swam with a more familiar stroke or were allowed to visualize swimming). Klapproth (2009) showed that memory mixing could happen using one modality only (visual), but it required the instructions to be ambiguous or misleading. In his experiment using temporal generalization, participants first learned two slightly different visual

standard durations. However, participants were either told that the standards were the same or different. The latter group was asked to use the shorter standard for the subsequent generalization task. There was also a control group who only received training on the shorter standard. Results showed that the temporal generalization peak of the 'same' group was displaced to the right relative to the other two groups (Experiment 1). However, when clearer instruction on which standard to use was given, participants could retrieve the relevant standard, indicating that distinct memories for each standard were maintained.

Response Time

Mean RTs during Session Single showed a consistent pattern with the previous experiments, showing a sudden decrease in the values of the ex-Gaussian parameters at probe durations exceeding the GM, and larger *Tau* at probe durations nearest to the GM.

Importantly, a modality effect was also detected. Analyses of *Mu* showed that auditory RT was shorter overall than visual RT in Session Single. This is consistent with better discrimination for auditory stimuli than visual stimuli. For instance, the sharper offset in the tone than the square, such that participants could detect the offset more accurately and emitted a response more quickly (Grondin, 1993); alternatively, an auditory stimulus may have a more arousing or stronger orienting power (Gaillard, 1976) such that reaction to the imperative stimulus is faster. For *Tau*, extreme RTs at Probe 3 did not differ from Probe 4 for auditory durations, while it did not different from Probe 4 and 5 for visual durations, suggesting that they sometimes identified longer visual durations as the same as the bisection criterion, consistent with the direction of the modality effect. However, the RT analysis did not reveal any difference between Group SD and DS, who showed different degree of the modality effect on perceived durations. This may be because given the time participants took to make a decision does not dictate whether the decision was a short or long response.

The CNV and the Modality Effect on Duration Estimation

ANOVAs on the whole CNV amplitude at fronto-central sites showed that auditory CNV was in general more negative than the visual CNV (e.g., Pfeuty et al., 2008). This was interpreted as the stronger orienting induced by auditory stimulation (Gaillard, 1976). Another possibility for the auditory CNV to be more negative is the superimposition of a sustained negativity due to continuous auditory stimulation by the filled tones and the medial-central negativity (Campbell et al., 2009; N'Diaye et al., 2004).

The next analyses of the CNV were guided by the two PSE effects documented in the psychometric parameter analyses. First, PLSC on the ERPs based on the session effect on PSE revealed non-significant LV in the amplitude difference for auditory probes and a significant LV for visual probes. Inspection of stable salience suggests that the difference occurred earlier in time and more posterior in topography for visual than auditory probes. The direction of the difference for the auditory probes is consistent with the pacemaker-interpretation of the CNV, since the longer bisection criterion in Session Double was associated with more negative amplitude at the CNV time window. In contrast, the difference for the visual probes was more related to the posterior slow perceptual component of visual stimulation, with the longer bisection criterion in Session Double associated with more positive amplitude. These results are far from conclusive for the pacemaker-accumulator interpretation of the CNV, with the different loci of differences in each modality implying that the modality effect in perceived time might have multiple origins, such as the contribution of perceptual cortical activity to timing (Bueti, Bahrami, & Walsh, 2008; Jantzen, Steinberg, & Kelso, 2005) and the different modes of attention (Berry, Li, Lin, & Lustig, 2013, see below).

Second, ANOVA analysis on the CNV amplitude showed that the CNV of group SD was more negative than group DS. This effect can also be seen in the PLSC

brain scores when Session Single was analyzed. Ladanyi and Dubrovsky (1985) and McAdam (1966) reported that better timers showed smaller CNV amplitude (Macar & Vidal, 2004). Therefore, group SD may be less adept in performing the duration bisection task and showed larger interference of timing between modalities. PLSC on the ERPs failed to reveal any discernable differences in the ERP time courses to account for the presence of the modality effect in half of the participants, but absence in the other half. The results are again inconclusive with regard to the pacemaker-accumulator model, as larger differences within group SD than within group DS were expected. The only result that showed some association between the CNV and the modality effect is that the visual CNV slopes near the PSE were less negative than the auditory CNV slopes, consistent with the assumption that the auditory clock runs faster than the visual clock, although this difference should have been independent of experimental condition. However, interpretation of the results is limited by the small sample size (N = 8 per condition due sample splitting) and inconsistent effects.

What the CNV may Reflect

Since more difficult timing tasks are associated with stronger SMA activation (Livesey et al., 2007), the larger negative potential observed in group SD collapsed across modalities may suggest that the CNV reflected difficulty related processes during duration estimation (McAdam, 1966). The shallower visual CNV slope observed only in group SD during Session Single might reflect slower attentional allocation when probes were visual, leading to delayed reaching of the bisection criterion and a larger modality effect in this group. In addition, similar to Experiment 2, the PCA results on the CSD data showed that the fronto-central negativity did not account for the sustained negativity; instead, it was the bilateral negativity, and it was present in both auditory and visual probe durations. Unlike Experiment 2, this PC was right lateralized, consistent with Coull et al.'s (2004) findings that the inferior frontal gyrus activation changed linearly with the amount of attention paid to the timing

aspect of a dynamic visual stimulus in a time-color dual task setting. However, a motor preparation interpretation cannot be ruled out because response hand was not counterbalanced in this experiment; the stronger right lateralization may be due to the preparation of a right hand response for answer Short at the beginning of each trial regardless of probe duration. On the other hand, the stronger negativity with auditory probe durations is consistent with the more 'automatically' attention capturing nature of auditory stimuli (Berry et al., 2013; Chen et al., 2010). This higher automaticity might also find support from the shorter ex-Gaussian *Mu*-s for the auditory probes.

The fact that the modality effect of perceived duration is closely tied to the different attentional demands for visual and auditory stimuli is demonstrated in (Berry et al., 2013), who investigated the relationship between timing, time-on-task, and subjective report on various attentional attributes using the modified Continuous Temporal Expectancy task (CTET), in which streams of visual or auditory stimuli were presented and participants had to respond when they detected the oddball stimuli with lengthened duration, while they were simultaneously distracted by an irrelevant video or not. The authors found that time-on-task, which taxed participants' sustained attention, interacted with the modality effect, such that the longer time-on-task, the larger the difference between modalities in the accuracy of detecting the oddball. On the other hand, performance in CTET correlated with different self-report attributes depending on the modality: visual CTET was correlated more strongly with distractibility and less with boredom, while auditory CTET showed the reversed pattern.

In conclusion, a modality effect on subjective time, indicated by a shorter PSE for auditory than visual stimuli, was found in Experiment 3. In addition, intermixing probe durations from different duration ranges also introduced a shift in the bisection criterion. For the modality effect, it was moderated by participants' knowledge about the task, as shown by the Session Order by Modality effect.

Examining the EEG differences focusing on the modality effect and the range effect did not reveal systematic changes in the CNV. The more negative CNV in auditory probes and the PCA results are consistent with a temporal attention and/or motor preparation interpretation of the CNV.

Chapter 6 General Discussion

The duration bisection task was used across three experiments to examine whether performance dependent changes in the CNV are consistent with a pacemaker-accumulator account of the perceptual-cognitive processes during interval timing.

In Experiment 1, the PSE, response time, and ERP data showed that participants could make a bisection decision once the elapsed time had exceeded the GM, implying the bisection criterion was at or close to the GM (Allan & Gibbon, 1991). The CNV data also implied that participants were sensitive to the passage of the short anchor. More specific to the pacemaker-accumulator account, although the CNV ramp rate correlated with the PSE, but the CNV amplitude did not show systematic changes to the difference in perceived time. Hence, it appears that the CNV time course reflects temporal decision making, but not necessarily the temporal memory as proposed in the pacemaker-accumulator account. Its time course before resolution may reflect essential, but non-temporal processes such as sustained attention and response uncertainty.

In Experiment 2, we observed the changes in the CNV time course when the Short anchor and the GM were shifted by conducting two bisection sessions with different S and GM values while keeping the task difficulty constant. Consistent with the pacemaker-accumulator account, the CNV slope was steeper when absolute durations were shorter (S = 605, L = 1852 ms). However, this CNV was also more negative than that obtained in the condition with longer anchor durations (1060 and 3240 ms), failing to support the claim that the CNV amplitude is a marker of a fixed accumulator threshold. In addition, the overall time course of the CNV was more peaked and ramp-like when absolute durations were shorter. PCA results suggested that the difference in CNV amplitude had a bilateral origin with a scalp distribution above the prefrontal and/or temporal cortices. These observations may be consistent

with the CNV reflecting processes such as temporal attention, anticipation, and motor preparation, but not the clock per se.

In Experiment 3, PCA results showed that the bilateral PC was similar regardless of stimulus modality. It also had a right prefrontal lateralization, consistent with an fMRI study showing that the inferior frontal gyrus may be responsible for temporal attention (Coull et al., 2004), although it might alternatively indicate early motor preparation, as participants expected to make a left index finger response, i.e., response Short, at the beginning of the trials. While these are essential functions for accurate and successful timed behaviors, none of these possibilities offer direct support to the claim that the CNV reflects a clock mechanism.

CNV and Time Perception

Sub-grouping epochs for probe durations that received comparable proportions of short and long responses failed to reveal a more negative CNV amplitude for durations classified as Long as compared to Short. When duration range or probe modality was manipulated, we also did not observe a more negative CNV when participants were assumed to hold a longer bisection criterion. We also did not obtain systematic difference in the CNV amplitude when we attempted to use the 'tones judged longer than lights' modality difference in perceived time to enhance differences in perceived time.

Regarding CNV resolution, although not always corresponding exactly with the bisection criterion, throughout three experiments we observed that the CNV never monotonically increased in negativity till the end when the probe durations were relatively long. Rather, the CNV always showed resolution or a gradual decrease in negative amplitude at or before the GM. Assuming a relationship between CNV resolution and the criterion time, it could be that participants break the durations into smaller portions to help them time (Grondin, Meilleur-Wells, & Lachance, 1999; van

Rijn & Taatgen, 2008), although one might argue that some of the durations used here were not long enough for chunking to be effective. Alternatively, the ramp and peaking of the CNV may reflect orienting to stimulus onset or setting up pre-timing thresholds (Boehm et al., 2012; Fujioka et al., 2012; Loveless, 1975), as the iCNV was originally interpreted. Further work is needed to better delineate the three CNV subcomponents researchers have proposed (Macar & Vidal, 2004). For instance, Monte et al. (2013) adapted a 'temporal oddball' task, in which participants attended passively to the presentations of three S1-S2 intervals (ISI) intermixed in the same block. Seventy percent of the ISIs were the 1500 ms standard duration, 15% were 2500 ms, and remaining 15% were 3000 ms. Results showed that the CNV resolved at about 1500 ms regardless of the magnitude of the deviant, implying that participants established temporal anticipation through implicit learning.

Using a temporal discrimination task, Kononowicz and van Rijn (2014) also showed that the CNV resolved early. However, modeling of single trial amplitudes with mixed regression revealed that the amplitude of the evoked potentials (N1P2) elicited by the offset markers of the empty auditory time intervals, but not the CNV, predicted the perceived time. Indeed, a model including the CNV was actually worse. van Rijn et al. (2011) pointed out that if the CNV amplitude reflected the internal standard in Macar et al.'s (1999) the reproduction task, then the opposite pattern should hold, i.e., the longer the reproduced duration, the *less* negative the CNV amplitude, because a less negative CNV would indicate shorter internal standard (fewer pulses), so that the participant felt that the criterion time had not been reached and prolonged their reproduced interval. Macar's et al.'s argument would require the CNV to reflect the temporal memory of the target duration used for a given trial, while van Rijn et al.'s argument would require the CNV to reflect the accumulation of current temporal evidence that may be separable from the to-be-compared target duration memory. Therefore, from an empirical and theoretical perspective, the

properties of the CNV may not be consistent with the pacemaker-accumulator account.

The formulation of how single-cell climbing neural firing patterns can be translated to scalp-level summated synaptic potentials was proposed relatively recently (Reutimann et al., 2004; Simen et al., 2011a,b). These formulations have their roots in perceptual decision-making models (John, 1967; Miller & Ulrich, 2003), specifically drift-diffusion models (Ratcliff & McKoon, 2007). They assume that perceptual information is noisy and can only be used as evidence for decision making by accumulating many such observations over time (see Zhang, 2012 for a review). A decision is made when the amount of evidence reaches one of the decision boundaries (e.g., Yes/No). Such models have been able to explain and predict behavioral performance such as reaction time (e.g., Ratcliff & McKoon, 2007), and account for decision differences based on physiological outputs (e.g., trial-by-trial variability in EEG, Ratcliff et al., 2009). An integration-to-boundary mechanism may account for the climbing electrophysiological signals in the CNV (e.g., Akkal et al., 2004; Durstewitz, 2003, 2004; Pfeuty et al., 2005; Simen et al., 2011a,b) and provide more quantitative predictions about the changes of the CNV given the assumed underlying timing mechanisms.

CNV Time Course and Temporal Anticipation

Although the CNV observed in Experiment 2 did not conform to a number of the predictions made by the pacemaker-accumulator account of CNV function, this does not mean that the CNV cannot reflect temporally sensitive processes. The degree of sustained attention and response uncertainty are undoubtedly governed by underlying timing mechanisms. On the other hand, the CNV may reflect implicit timing, the detection and use of temporal information unconsciously or without the need for deliberate effort (e.g., temporal orienting). Prospective explicit and implicit timing share different yet overlapping neural networks (Coull & Nobre, 2008);

behaviorally they also share highly similar properties (e.g., scalar property; Piras & Coull, 2011). The CNV seems to reflect both kinds of temporal processing (e.g., Miniussi et al., 1999).

Qualitatively, the CNV we found corresponded with the degree of temporal anticipation in each session. Referring to the CNVs obtained in Experiment 2, their time courses showed some resemblance to subjective anticipation functions (Fig 6.1) constructed based on the equations given in Janssen and Shadlen (2005). These functions are characterized by early peaks near S, different density 'heights', and gradual resolution. This speculation is consistent with findings showing that the CNV is sensitive to the conditional probability of the foreperiods (FP, Cravo, Rohenkohl, Wyart, & Nobre, 2011; Trillenberg et al., 2000). In variable FP conditions, RTs decrease as a function of the FP duration (Niemi & Näätänen, 1981). By varying the probability of the occurrence of each of the FPs, researchers can manipulate participants' subjective anticipation (posterior probability) about when a target stimulus would be more likely to occur (Janssen & Shadlen, 2005; Nobre, Correa, & Coull, 2007). Using three different distributions with three FPs (1300, 1950, and 2600 ms) in a cued simple reaction time task, Trillenberg et al. (2000) found that changes in the CNV amplitude matched qualitatively with the change in posterior probability and RT, being maximal at FPs for which a target was most likely. Using a go/no go reaction time task, Cravo et al. (2011) also observed a similar relationship between CNV amplitude and FP using similar intervals. Janssen and Shadlen (2005) reported single cell activity in monkeys that followed these anticipation functions closely.

In typical timing tasks, the number of trials per probe duration is usually the same. This would result in higher temporal anticipation at the central tendency of the durations as shown in Figure 6.1. Since changing the number of trials per probe duration will also change the GM/AM of the whole probe distribution (Brown et al., 2005; Raslear, 1985; Wearden & Ferrara, 1996), observing how the CNV changes in

an explicit timing task when the distribution of the probe duration changes may tell us how explicit and implicit timing interact (e.g., Los & Heslenfeld, 2005).

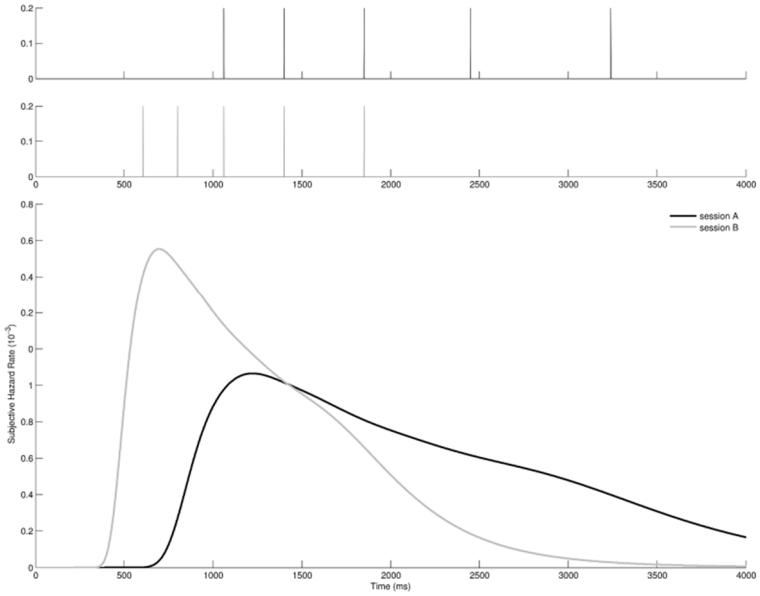


Figure 6.1. Probability of probe durations in Session Long (top) and Session Short (middle). Bottom: Subjective anticipation functions of Session Long (black) and Short (grey), using a Weber fraction of .15, which is the mean WF.

Positive Components and Time Perception

We showed the modulation of the offset positive component, which resembles the P200/P300, as a function of response, and attributed the difference of this component between durations classified as Short and Long to decision making processes (cf. Lindbergh & Kieffaber, 2013). Some researchers have further posited the function these late positive components may imply (Gibbons & Rammsayer, 2005).

The analyses and discussions have focused on the relationship between the CNV and the criterion time estimation, but analysis of temporal sensitivity (DL and WF) was also provided. At least one fMRI study has shown that the signals from some key neural structures exhibit the Scalar property (Hinton, 2003). On the other hand, a relationship between temporal sensitivity and the positive component of the

stimulus offsets has been reported previously. Gibbons and Stahl (2008) asked participants to perform temporal reproduction of a 2-second empty auditory target duration as accurately as possible. Timing performance was evaluated by median split of the sample based on either mean reproduction accuracy (absolute error) or variation of reproduction (coefficient of variation, CV). Specifically, the amplitude at Cz of the P300 elicited by the standard interval offset was more positive in the group with less varied reproductions (smaller CV). There was also a negative correlation between this offset P300 and CV. Consistent with their two-stage model of the temporal generalization task (cf., Gibbons & Rammsayer, 2005), the authors proposed that the offset P300 during the target presentation indicated a comparison between the presented target and the internal representation of the target. Thus, participants did not passively attend to the presented target, but actively revised their internal representation when necessary. It follows that better performers engaged in such processes more efficiently, forming more accurate expectations about the time of offset of the target duration, thus giving rise to larger offset P300 amplitudes. Paul at al. (2011) interpreted a more positive late component (using average reference) at the frontopolar electrodes in a more difficult temporal discrimination task (closely versus widely spaced probe durations) as reflecting more effortful decision making.

As positive slow waves such as the P300 reflect attentional allocation due to different memory updating demands (Polich, 2010), further study of the negative (CNV) and positive (P3) slow wave network may provide more detailed information about how temporal memory is formed and influenced by incoming temporal information. For instance, Gibbons and Stahl (2008) further found that participants with a smaller absolute error (deviation of the mean reproduction from 2 seconds) showed a more negative CNV. However, these participants were not necessarily the good timers, because their reproduction variability was not necessarily smaller than the other participants. The authors proposed that these participants may use more

trial-by-trial strategies to correct for their reproduction deviations instead of relying on a stable internal representation of 2 seconds (as what a good timer would do). This strategy is more effortful, resulting in a larger CNV (e.g., Livesey et al., 2007).

Methodology

As discussed earlier, study of response times in interval timing tasks can corroborate and extend findings based only on timing parameters (Gu & Meck, 2011; Kristofferson, 1977; Lindbergh & Kieffaber, 2013; Los & Heslenfeld, 2005; Penney, 2004; Rousseau & Rousseau, 1996; Taatgen, van Rijn, & Anderson, 2007). Furthermore, temporal decision is being reconciled with other perceptual decision making, a lot of which has been explained well by drift diffusion models (Balci et al., 2011; Ratcliff & McKoon, 2007). As briefly mentioned above, this model family includes a starting point, an evidence collection rate (drift), and one or more decision boundaries. Some groups have successfully put time perception under this family (Simen et al., 2011a,b, 2013). With RT being the most important variable in this line of research, we can expect that studying RT in properly designed timing tasks such as duration reproduction will offer additional insights about time perception (MacDonald & Meck, 2004, 2006). Simen et al. (2013), for instance, have made specific predictions regarding the skewness of RT and its relation to temporal variability under their neurologically realistic pacemaker-accumulator type timing mechanism.

The versatility of the multivariate PLSC analysis was demonstrated in its ability to explore the spatiotemporal neurodynamics of scalp EEG recordings and provide statistical inference. A combination of such 'exploratory' methods with more focused 'region of interest' univariate approaches can be a useful compromise between data reduction and sensitivity to the effects of interest. This emphasis of awareness of the 'global' signals can also be seen in other non-traditional approaches such as topographical, GFP, and micro-state analyses (e.g., Koenig, Kottlow, Stein, &

Melie-García, 2011; Murray et al., 2008). These analyses can provide alternatives to previously intractable problems in scalp EEG analysis.

Future Directions

The weaker manifestation of the CNV-accumulator relation observed in this dissertation may not be too surprising if one believes that the bisection task is easy enough that a fuzzier temporal memory is sufficient for good task performance (Droit-Volet, 2003). This possibility can be examined by using more difficult versions of the bisection task (e.g., using smaller S:L ratio; Penney et al., 2008; Wearden & Ferrara, 1996). Admittedly, different timing tasks may place different demands on the various temporal and non-temporal task characteristics (e.g., absolute or relative time judgment, reliance on short term and/or long term memory, active or passive monitoring of time; Zakay & Block, 1997). This explains, for example, why performance across different time perception tasks is correlated in general, but sometimes only moderately (Bangert, Reuter-Lorenz, & Seidler, 2011; Merchant, Zarco, & Prado, 2008); why some populations can perform one kind of task, but not another (Allman & Meck, 2012; Koch, Oliveri, & Caltagirone, 2009; Toplak, Dockstader, & Tannock, 2006). While we argued that the bisection task is a good candidate as a validation task for the pacemaker-accumulator interpretation of the CNV based on the experimental findings discussed in Chapter 2 and our empirical behavioral findings, more direct evidence of the temporal memories used in the bisection task is desirable, as it will inform researchers whether there is a unified cognitive model to describe timing across a wide range of timing tasks (e.g., Coull & Nobre, 2008; Merchant et al., 2008; Wearden, 2004).

In Experiment 2, changing absolute durations permitted manipulation of the bisection criterion. To corroborate or refute the conclusions reached from the current findings, manipulations for changing the criterion without changing the range of

durations or S and L and maintaining the S:L ratio, such as that used in Brown et al. (2005; see also e.g., Raslear, 1985), would be useful.

In Experiment 3, the unexpected session order effect complicated the interpretation of the data. The outcome of using the session Double as a control for session Single was also problematic, because a mixing effect was also evident in session Double. Since visual timing is supposed to be more attention demanding and more susceptible to the influence of auditory timing than vice versa, a simplified control condition may be set up in which only visual timing was performed, and the ERP differences between the visual timing in dual modality and single modality condition may be compared to yield more clear results.

Finally, similar to the current project, a number of previous findings supporting the pacemaker-accumulator interpretation of the CNV have a prominent motor component in their paradigms. Since the CNV, the SMA, and timing are all closely tied to successful motor actions (Bueti & Walsh, 2009), it will be of interest to tease out the motor aspect of the CNV as much as possible and to re-examine the extent the CNV reflects the clock mechanism, as illustrated in Monte et al. (2013).

In conclusion, we showed that the duration bisection task elicited similar ERP components as other conventional timing perception tasks. The EEG and behavioral data displayed patterns suggesting that participants seem to time the arrival of the bisection criterion (PSE) that is close to the GM. In contrast to the pacemaker-accumulator and climbing neural firing hypotheses, the changes in the CNV time course and amplitude may reflect important functions such as sustained attention, orienting and establishing some neural threshold rather than reflecting the underlying clock (van Rijn et al., 2011). Analyses encompassing both the negative and positive slow waves may enable a more thorough investigation of time estimation and temporal decision making (Gibbons & Rammsayer, 2005). Such understanding will

also benefit from including more behavioral indicators such as response time (Gu & Meck, 2011).

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